



RECORDS OF THE AUSTRALIAN MUSEUM



Volume 38 Contents

RECORDS OF THE AUSTRALIAN MUSEUM

Editor:

J.K. Lowry

Assistant Editors:

L.H. Hodgson
S.J. Hand

Associate Editors:

Anthropology:

R.J. Lampert

Invertebrates:

W.F. Ponder
D.K. McAlpine

Geology:

F.L. Sutherland

Vertebrates:

J.M. Leis

The Australian Museum has published natural science papers from the Australian area since 1890. The *Memoirs of the Australian Museum* (1890-1982) have now been replaced by the *Supplement* series to the *Records of the Australian Museum*.

The *Records* publish original research in the fields of anthropology, geology and zoology. Small papers or monographs which are relevant to Australia, the South-west Pacific and the Indian Ocean area may be submitted. Research based on Australian Museum collections or by museum staff may be given priority. All submitted manuscripts are reviewed by external referees. The publication is distributed to scholarly institutions throughout the world.

Submitted manuscripts should be addressed to the Editor and exchange enquiries to the Librarian, Australian Museum, P.O. Box A285, Sydney South, N.S.W. 2000, Australia.

Subscription information.

Records of the Australian Museum is published three times a year, each issue consisting of two numbers. The annual subscription is \$A100.

Supplements are published irregularly. They are not covered by subscriptions to *Records* and are priced according to size. Coming *Supplements* are announced in *Records*.

Orders for *Records* and/or *Supplements* from Australia, New Zealand and New Guinea should be addressed to the Circulations Officer (Community Relations), Australian Museum, P.O. Box A 285, Sydney South, N.S.W. 2000, Australia. Orders from other countries should be addressed to E.J. Brill, Postbus 9000, 2300 PA Leiden, Netherlands.

© Copyright Australian Musuem, 1986.
No part of this publication may be reproduced without permission of the Editor.

Produced for the Australian Museum by
Love Computer Typesetting Pty Ltd

CONTENTS

Volume 38

BICKEL, DANIEL J. <i>Thrypticus</i> and an allied new genus, <i>Corindia</i> , from Australia (Diptera: Dolichopodidae)	135
—— Australian species of <i>Systemus</i> (Diptera: Dolichopodidae)	263
CHOAT, J. HOWARD & JOHN E. RANDALL. A review of the parrotfishes (family Scaridae) of the Great Barrier Reef of Australia with description of a new species	175
FAUCHALD, KRISTIAN. Review of the types and key to the species of <i>Eunice</i> (Eunicidae: Polychaeta) from the Australian region	241
GLASBY, CHRIS. See Hutchings, Pat	105, 319
GRIFFIN, D.J.G. & H.A. TRANTER. Some majid spider crabs from the deep Indo-West Pacific	351
HUTCHINGS, PAT & CHRIS GLASBY. A revision of the genus <i>Euthelepus</i> (Terebellidae: Thelepiniae)	105
—— The Polycirrinae (Polychaeta: Terebellidae) from Australia	319
KORNICKER, LOUIS S. <i>Codonocera cuspidata</i> , a new species of pelagic ostracode from off Queensland, Australia (Crustacea: Ostracoda: Cypridinidae)	119
MYERS, A.A. Amphipoda from the South Pacific: Tonga	271
PAXTON, HANNELORE. Generic revision and relationships of the family Onuphidae (Annelida: Polychaeta)	1
—— Revision of the <i>Rhamphobrachium</i> complex (Polychaeta: Onuphidae)	75
RANDALL, JOHN E. See Choat, J. Howard	175
THEISCHINGER, G. Australian Thaumaleidae (Insecta: Diptera)	291
TRANTER, H.A. See Griffin, D.J.G.	351
WATSON RUSSELL, CHARLOTTE. <i>Paleaequor</i> , a new genus of Polychaete worm (Chrysopetalidae)	153

Produced for the Australian Museum by
Love Computer Typesetting Pty Ltd



P507
A938

Generic Revision and Relationships of the Family Onuphidae (Annelida: Polychaeta)

HANNELORE PAXTON

School of Biological Sciences, Macquarie University,
North Ryde, NSW 2113, Australia.

ABSTRACT. The general morphology, reproduction and development of the family Onuphidae are reviewed and supplemented with new observations, emphasizing ontogenetic changes. The following features were found to be associated with the juvenile state: distinctive colour pattern, ceratophores of antennae with few rings, absence of frontal palps and tentacular cirri, presence of eyes, smaller number of modified setigers, lesser developed branchiae, early occurrence of subacicular hooks, presence of compound falcigers in anterior and far posterior setigers.

Five new genera are described, bringing the number of recognized genera in the family to 22. A key, diagnoses and illustrated definitions to all genera are given.

The relationships within the family are analyzed using morphological, ecological and life history characters. Two subfamilies: Hyalinoeciinae, n. subf., and Onuphinae are erected. The two subfamilies differ in the presence or absence of notosetae, position of subacicular hooks and lower limbate setae, number of anal cirri, primary envelope of oocytes and arrangement of their nurse cells. Two groups of genera are recognized in each subfamily. The Hyalinoeciinae includes the *Nothria* group (consisting of *Nothria* and *Anchinothria*, n. gen.) and the *Hyalinoecia* group (consisting of *Hyalinoecia*; *Leptoecia*; *Neonuphis*; *Hyalospinifera*). The Onuphinae includes the *Diopatra* group (consisting of *Notonuphis*; *Paradiopatra*; *Diopatra*; *Epidiopatra*; *Brevibrachium*, n. gen.; *Longibrachium*, n. gen.; *Rhamphobrachium*; *Americonuphis*) and the *Onuphis* group (consisting of *Australonuphis*; *Hartmanonuphis*, n. gen.; *Hirsutonuphis*, n. gen.; *Aponuphis*; *Kinbergonuphis*; *Mooreonuphis*; *Onuphis*; *Heptaceras*).

It is hypothesized that the Onuphidae have a southern centre of origin and radiated from epifaunal habitats to world-wide distributions from the shallowest to the deepest depths.

PAXTON, HANNELORE, 1986. Generic revision and relationships of the family Onuphidae (Annelida: Polychaeta). Records of the Australian Museum 38(1): 1-74.

CONTENTS

INTRODUCTION	2
MATERIALS AND METHODS	3
GENERAL MORPHOLOGY	4
Prostomium	5
Peristomium	9
Parapodia	9
Setae	12
Eversible Pharynx	14

Pygidium	16
Tubes	16
Size	16
REPRODUCTION AND DEVELOPMENT	16
Reproduction	16
Juvenile Development	18
General Juvenile Characters of Onuphidae	19
TAXONOMIC ACCOUNT	22
Key to Genera of Onuphidae	23
Family Onuphidae	25
Hyalinoeciinae n. subf.	25
<i>Nothria</i> Malmgren	25
<i>Anchinothria</i> n. gen.	27
<i>Hyalinoecia</i> Malmgren	29
<i>Leptoecia</i> Chamberlin	30
<i>Neonuphis</i> Kucheruk	32
<i>Hyalospinifera</i> Kucheruk	34
Subfamily Onuphinae	35
<i>Notonuphis</i> Kucheruk	35
<i>Paradiopatra</i> Ehlers	36
<i>Diopatra</i> Audouin & Milne Edwards	38
<i>Epidiopatra</i> Augener	41
<i>Brevibrachium</i> n. gen.	41
<i>Longibrachium</i> n. gen.	43
<i>Rhamphobrachium</i> Ehlers	44
<i>Americonuphis</i> Fauchald	45
<i>Australonuphis</i> Paxton	46
<i>Hartmanonuphis</i> n. gen.	49
<i>Hirsutonuphis</i> n. gen.	51
<i>Aponuphis</i> Kucheruk	53
<i>Kinbergonuphis</i> Fauchald	54
<i>Mooreonuphis</i> Fauchald	56
<i>Onuphis</i> Audouin & Milne Edwards	56
<i>Heptaceras</i> Ehlers	58
PHYLOGENETIC RELATIONSHIPS	60
Discussion of Characters and Their States	61
Relationships Within the Onuphidae	65
Identikit Picture of the Uronuphid	68
ZOOGEOGRAPHY AND CONCLUSION	68
ACKNOWLEDGEMENTS	70
REFERENCES	70

Members of the family Onuphidae (order Eunicida) are mostly tubicolous, range from a few centimetres to the longest polychaetes ever reported (3 metres) and occur in all oceans from intertidal to the deepest depths. Onuphids used to be considered as predominantly deep-water species (McIntosh, 1910) that lived permanently in rather sturdy tubes (Pettibone, 1963). However, many shallow water species with fragile tubes are now known (Fauchald, 1980). A number of species, some of large size with very fragile, temporary tubes occur in sandy beaches, predominantly in the southern oceans. The largest of these, species of *Australonuphis*, occur in

Central and South America and in eastern Australia. They are known as 'beachworms' in Australia and are highly sought after for fishing bait, collected from surf beaches during low tides by amateurs and professional collectors. The study of these beachworms (Paxton, 1979) has led to the present revision of the family.

Order Eunicida. The order Eunicida includes seven of the 81 extant families of polychaetes (Fauchald, 1977) and eight of the extinct families (Kielan-Jaworowska, 1966). Members of the order share the possession of a ventral eversible pharynx with a complex jaw apparatus consisting of ventral mandibles and dorsal maxillae. The

jaws are composed, to a large extent, of calcium and magnesium carbonates and, to a smaller extent, of sclerotized proteins (Jeuniaux, 1975). The jaw apparatus is an autapomorphic feature, marking the Eunicida as a monophyletic group. Although a number of other polychaete families have jaws (see Wolf, 1976), their chemical composition differs markedly from that of the Eunicida, suggesting that the Eunicida represent a "phylogenetic line distinct from that of other 'errant' predacious polychaetes" (Voss-Foucart *et al.*, 1973).

The jaw apparatuses of Eunicida consist of four types: Placognatha (Kielan-Jaworowska, 1966), Ctenognatha (Kielan-Jaworowska, 1966), Prionognatha (Ehlers, 1868) and Labidognatha (Ehlers, 1868). The former two types are characterized by having rows of maxillae with gaping basal cavities. The placognath type is extinct, while the ctenognath type is represented by one extant family, the Dorvilleidae. Prionognatha and Labidognatha have fewer maxillae with much reduced basal cavities. The two halves of the prionognath type maxillae are more or less symmetrical and arranged in parallel rows; extant families are the Arabellidae and Lysaretidae. The labidognath type maxillae are asymmetrical and so arranged as to form a semicircle in the retracted state; extant families are the Lumbrineridae, Iphitimidae, Arabellidae, Lysaretidae, Eunicidae and Onuphidae.

The Eunicida has been treated as a family (Ehlers, 1868; Fauvel, 1923; Day, 1967), superfamily (Kinberg, 1865; Hartman, 1944; Fauchald, 1970) or order (Dales, 1962; Fauchald, 1977); the last mentioned is followed in this paper. Historical reviews of the taxonomic studies on the Eunicida can be found in McIntosh (1910) and Hartman (1944). The phylogeny of the fossil Eunicida has been discussed by Kielan-Jaworowska (1966). She concluded that the placognath and ctenognath maxillae, which were well established by the Ordovician, were the most primitive types. She stated that Recent prionognath families could be derived from several extinct prionognath families, while the Recent labidognath families—Eunicidae, Onuphidae and possibly Lumbrineridae—arose from the Palaeozoic Paulinitidae. The relationships between the extant families have never been elaborated. However, the similarity between larval onuphid and eunicid maxillae and adult dorvilleid maxillae has been interpreted as an indication of the ancestral position of the Dorvilleidae (Monro, 1924).

Family Onuphidae. The family Onuphidae was erected by Kinberg (1865) as 'Onuphiæa' and has remained unchanged, although it was treated as a subfamily by several authors (McIntosh, 1910; Fauvel, 1923; Day, 1963). Kinberg erected the family for those members of his superfamily Eunicea with 7 maxillae, 5 tentacles, 2 antennae, 2 palps and a single buccal segment, to contain the genera *Onuphis* and *Diopatra*. The number of genera increased rapidly to a dozen by 1919. This number remained the same for more than 50 years, with most authors accepting only eight to ten (e.g. Hartman, 1944, 1945; Day, 1967).

The characters employed for generic separation were presence or absence of tentacular cirri, presence or absence of branchiae, and the structure of branchial filaments when present. The modification of the anterior parapodia and their specialized setae were generally not used as characters, except for *Rhamphobrachium* Ehlers, 1887.

About 220 species have been described; most of these have been in the genera *Onuphis* and *Nothria*, which contained 60 and 40 species respectively as accepted by Fauchald (1977). The division between *Onuphis* and *Nothria* on the basis of their branchial structure (*sensu* Hartman, 1944) was presumed artificial (Fauchald, 1968) but was retained for convenience. The unsatisfactory state of the generic classification was expressed repeatedly (e.g. Hartman, 1944; Pettibone, 1970).

A new phase of revisionary work started in the 1970's with redefinitions of *Nothria* and *Paradiopatra* by Pettibone (1970). New genera were described by Fauchald (1973), Orensanz (1974) and Hartmann-Schröder (1975). The most extensive revisions were carried out by Kucheruk (1978) and Fauchald (1982a). Kucheruk remarked on the unsatisfactory characters of earlier definitions and included the setae and nature of the tubes to arrive at a more natural classification. He described three new genera and gave definitions and a key to all genera. He remarked on the polyphyletic nature of the genus *Onuphis*, but did not attempt to subdivide it. Fauchald (1982a) revised the genera *Onuphis*, *Nothria* and *Paradiopatra* based on type material. By using the structure and length of antennae and putting more emphasis on setal structures, he redefined *Onuphis* and described three new genera (*Kinbergonuphis*, *Mooreonuphis*, *Sarsonuphis*), bringing the number of nominal genera to 24.

Cladistic analyses, although uncommon in polychaete studies, have been carried out to establish intrageneric (Westheide, 1977) and intergeneric relationships (Westheide, 1982; Westheide & Riser, 1983; ten Hove, 1984). Fauchald (1982a) used cladistic techniques to arrange the onuphids studied by him in patterns suggesting relationships within and between the genera examined, but the relationships between all genera of the family Onuphidae have never been examined.

The aim of the present study is to carry out a generic revision of the family Onuphidae. The study has three main objectives: (1) to provide an account of the comparative morphology and ontogenetic changes of the family; (2) to define the taxa on a wider range of characters; and (3) to elucidate the phylogenetic relationships within the family.

MATERIALS AND METHODS

This study is based mainly on museum collections. The material examined consists of type species (whenever possible), Australian species, and selected species from other geographic areas. Abbreviated collection data for the material examined is listed with

the respective genera, except for *Brevibrachium*, *Longibrachium* and *Rhampobrachium*. Full collection data for these genera are given together with species descriptions in Paxton (1986).

The order of taxa is according to the classification recognized in this study. Body length (measurements and numbers of setigers) of incomplete specimens are followed by plus signs, width is of setiger 10 without parapodia. All drawings were prepared with the aid of a camera lucida.

Scanning electron microscopy (SEM) examination was carried out on specimens originally fixed in formol saline. Specimens were dehydrated in a graded ethanol series, dried in a Sorvall critical point dryer using liquid CO₂, and gold coated in a Polaron sputter coating system. They were photographed in a JSM-T20 using a Robinson backscattered electron detector.

The observed ontogenetic changes of *Rhampobrachium* Ehlers, 1887 are based on 20 specimens of *R. ehlersi* Monro, 1930, and 29 specimens of *R. sp.* The length for each *R. ehlersi* stage is based on a single complete specimen (except stage 4 where no complete specimens were available), while the width is based on several incomplete specimens.

Taxonomic account. Differential diagnoses and definitions are given for all taxa. The species recognized as members of a genus are listed under 'remarks'. This information is provided for most genera, except those in need of revision, and is based on the literature and examination of specimens. The species listed include a number of new species from Australia which will be described in a forthcoming paper (Paxton, in preparation).

All keys are artificial and for adults only. A key to genera is given, as well as keys to species for a number of genera of particular interest to the author. Reference is made to recently published keys for other genera. However, no keys are available for a number of genera which are in need of revision.

Phylogenetic relationships. A brief outline of the theory and terminology of cladistic analysis, and its application to polychaetes can be found in ten Hove (1984).

The character states were determined by fossil evidence from the literature, ontogenetic changes observed in this study, and outgroup comparison. The outgroup comparison was based on examination of species of Eunicidae (listed below) and information from the literature: *Eunice aphroditois* (Pallas, 1788)—**Australia:** New South Wales—2 (AM W.1765-6) and others. *E. australis* Quatrefages, 1865—**Australia:** Western Australia—1 (AM W.5642). *E. tubifex* Crossland, 1904—**Australia:** New South Wales—1 (AM W.3528); **New Caledonia**—1 (AM W.198980). *Marphysa sanguinea* (Montagu, 1815)—**Australia:** New South Wales—2 (AM W.4881) and others. *Nematonereis unicornis* (Grube, 1840)—**Australia:** Queensland—2 (AM W.199003) and others.

A Wagner tree was constructed using a programme

by George McKay (MU) modified from Farris (1970). Autapomorphies were included in the analysis to define endbranches; a hypothetical, all-primitive ancestor was included.

Abbreviations

AHF	Allan Hancock Foundation, Los Angeles, Calif., U.S.A.
AM	Australian Museum, Sydney, NSW, Australia
BMNH	British Museum (Natural History), London, U.K.
CM	Canterbury Museum, Christchurch, New Zealand
MU	Macquarie University, North Ryde, NSW, Australia
MCZ	Museum of Comparative Zoology, Cambridge, Mass., U.S.A.
MNHP	Museum National d'Histoire Naturelle, Paris, France
NMV	Museum of Victoria, Melbourne, Vic., Australia
NMW	Naturhistorisches Museum Wien, Austria
NZOI	New Zealand Oceanographic Institute, Wellington, New Zealand
PML	Portobello Marine Laboratory, Portobello, New Zealand
QM	Queensland Museum, Brisbane, Qld, Australia
RNH	Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands
UC	University of Canterbury, Christchurch, New Zealand
UNC	University of North Carolina, Chapel Hill, N.C., U.S.A.
UNH	University of Hawaii, Honolulu, Hawaii, U.S.A.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.
UT	University of Tromsø, Tromsø, Norway
WAM	Western Australian Museum, Perth, WA, Australia
ZMB	Zoologisches Museum, Berlin, E. Germany
ZMH	Zoologisches Institut und Zoologisches Museum, Hamburg, W. Germany
ZMO	Zoologisk Museum, Oslo, Norway

GENERAL MORPHOLOGY

Some notes on the general morphology of onuphids can be found in most polychaete treatises and onuphid revisions. The aim of this section is to bring the information together, to supplement it with new observations, and to detail the characters utilized in the taxonomic accounts below. The general characters of Onuphidae are discussed and illustrated with reference to one of the earliest described and best known species, *Onuphis eremita* Audouin & Milne Edwards, 1833 (Figs 3, 6-8, 10) and other species examined in this study.

Colour patterns. While pigments are usually lost through preservation, onuphids often have a dark brown pigmentation that remains. The patterns are prominent in shallow-water forms, where they may consist of a pigmented peristomium and dorsal bands on the anterior segments (Fig. 34m).

Body shape. The anterior part of the body is generally cylindrical due to accommodation of the eversible pharynx (Fig. 1). Fauchald (1982a) stated that the median and posterior parts have one of three different body shapes: (1) slight dorsal flattening, almost circular in transverse section; (2) strong dorsal flattening, semicircular in transverse section; (3) convex dorsal and ventral surface, oval in transverse section. He related (1) and (2) to the development of branchiae and stated that species of (1) have poorly developed branchiae and fit closely into their tubes, while those of (2) have well developed branchiae. This categorization appears justified as far as permanent tube dwellers are involved. Animals of (1) need little space to aerate their branchiae (*Onuphis holobranchiata*, Fig. 2a), while animals of (2) need more space to use their branchiae efficiently (*Diopatra aciculata*, Fig. 2b). However, it may be a function of size since animals of (1) are generally smaller than those of (2). Many shallow-water species with fragile temporary tubes live in sandy beaches and have been termed beachworms (Paxton, 1979). Although these species have well developed branchiae, some are of (1) (*Onuphis eremita*, Fig. 2c), others of (2) (*Hirsutonuphis mariahirsuta*, Fig. 2d). Beachworms have very well developed longitudinal muscles, particularly the ventral bundle.

Species of *Nothria* (Fig. 2e) and allied forms with flattened tubes were considered as group (3) by Fauchald. The species examined in this study are more or less oval in transverse section; however, their ventral surface is not convex but flat. Their longitudinal muscles are extremely reduced.

The type of body shape may not only be related to the branchial development but also to the size of the animal, its mode of living (tubicolous or burrowing) and associated specializations (e.g. muscular development).

Prostomium

The prostomium is oval to rounded, usually wider than long. Anteriorly it can be smoothly rounded (Fig. 27a), slightly incised (Fig. 34a), or extended (Fig. 3b). The prostomial appendages consist of five dorsal antennae and a pair of frontal and ventral labial palps each.

Antennae. The antennae have been termed 'occipital tentacles' (Hartman, 1944; Fauchald, 1968) or 'occipital antennae' (Day, 1960; Fauchald, 1982a). Since they are the only antennae, the term occipital is redundant. The individual antennae have been referred to as 'paired outer and inner lateral' and 'median unpaired' (Hartman, 1944; Fauchald, 1968; 1982a). The term 'outer lateral' is misleading since their position is more often anterior (e.g. *Onuphis*) rather than lateral (e.g. *Rhamphobranchium*) to the second pair. It is preferable

to refer to the five antennae as (1) pair of anterior lateral, (2) pair of posterior lateral and (3) single median.

The antennae often form a crescent over the posterior half of the prostomium; in *Rhamphobranchium* and *Paradiopatra* this crescent has shifted more anteriorly. Fauchald (1982a) noted that in most *Nothria* and *Paradiopatra* (= *Anchinotiria*) the two anterior antennae are in a more anterior and median position and form a circle with the frontal palps when viewed from the dorsal side. This arrangement is not limited to these two genera, but occurs in most. Sometimes the anterior antennae are placed so far forward as to be in a ventral position (Fig. 30b). In the shallow-water genera the antennae are very thick, almost covering the dorsal part of the prostomium. While in most genera the median antenna is the most posteriorly placed, in *Heptaceras* (Fig. 36a) the median antenna has moved anteriorly and is placed centrally among the five.

The antennae consist of proximal ceratophores and distal styles. Although CERATOPHORES may be smooth in small species, they usually have circular constrictions, giving them an annulated or ringed appearance. The constrictions usually terminate subdistally, so that the terminal ring is several times as long as the others. The ceratophores range from short (2–3 rings) to very long (more than 30 rings). While the former are shorter than the prostomium, the latter are several times its length. The number of rings is reasonably constant (± 5) in most genera. Some small species of *Onuphis*, *Epidiopatra* and *Diopatra* have relatively few rings (5–10) while most have 15–20. The greatest variation is found in *Heptaceras*, where the number ranges from 20–60.

Some species of *Diopatra*, *Epidiopatra* and *Paradiopatra* have lateral projections on the ceratophores of the posterior lateral and median antennae (Fig. 24k) which Day (1960) considered as branching. These are limited to small species and may represent a neotenic condition.

The STYLES range from short (Fig. 30c) to moderately long (Fig. 3a) to very long (*Hyalinoecia*). The anterior lateral pair is the shortest, sometimes shorter than its ceratophore (Fig. 3a). The posterior lateral styles may be equal, shorter or longer than the median one. While the overall length of styles is relatively constant for some genera, in others there is considerable variation.

The styles are covered by combined sensory/secretory structures referred to as 'Sinnesknospen' or sensory buds by Pflugfelder (1929). He described their histology for *Diopatra* sp., showing that cilia project through the cuticle from a central sensory cell and that the ciliated cell is accompanied by one or two serous glands opening to the surface. SEM photomicrographs show that the sensory buds, although at times very inconspicuous, are present in all species of Eunicidae and Onuphidae examined. In most genera they are irregularly scattered (Fig. 4a,b), while in species of *Diopatra* the sensory buds are arranged in rows (Fig. 4c,d). The serous glands and their openings can be more numerous than in the species examined by Pflugfelder and are present as a semicircle

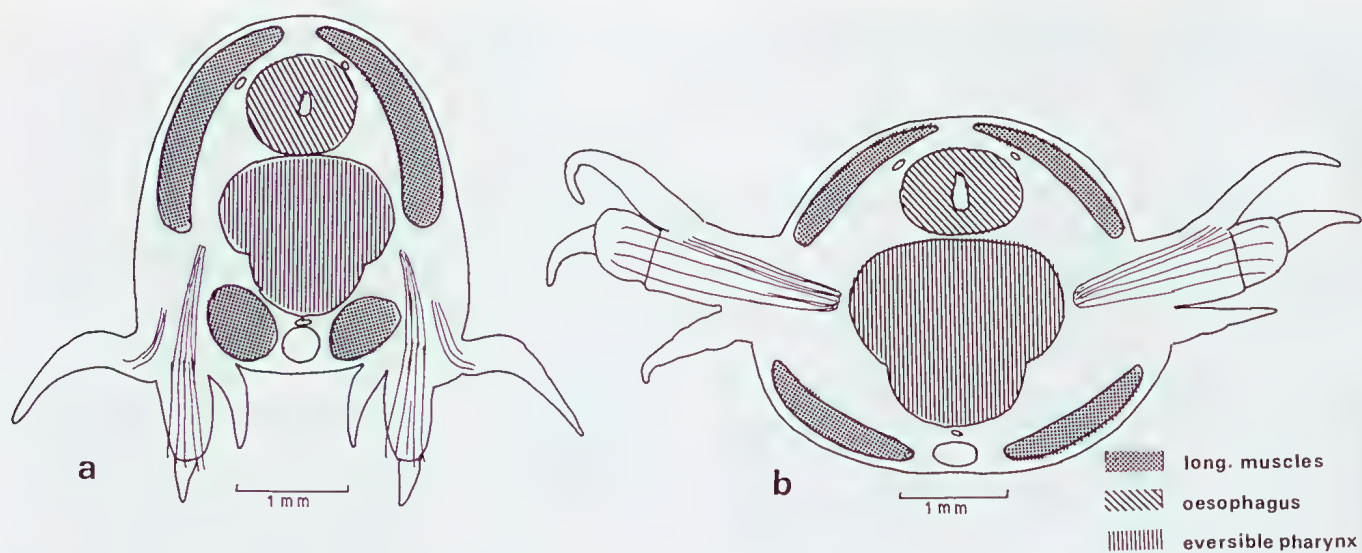


Fig. 1. Transverse sections through proboscideal region: a, *Diopatra* n. sp. 2, setiger 4; b, *Australonuphis teres*, setiger 3.

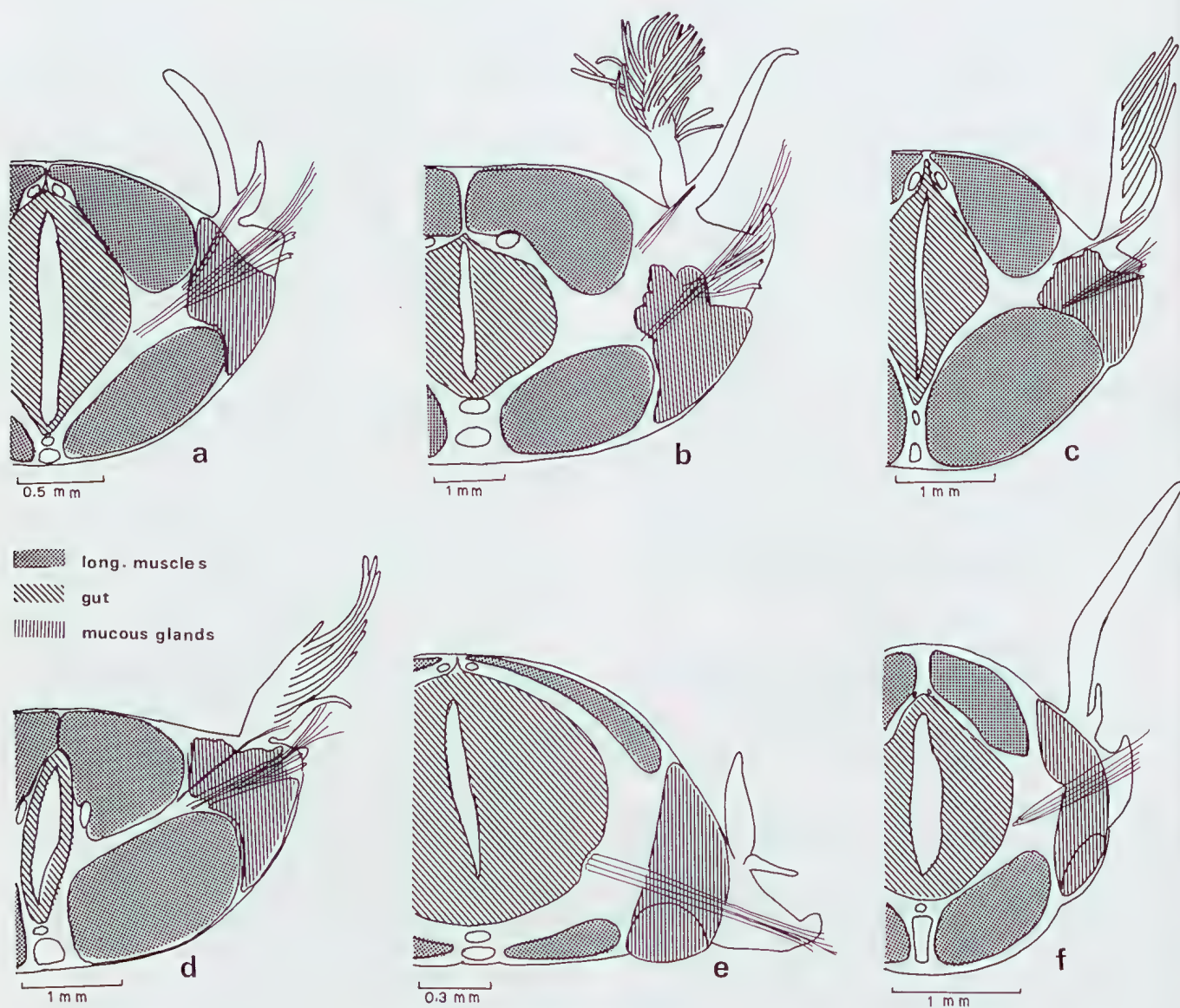


Fig. 2. Transverse sections: a, *Onuphis holobranchiata*, setiger 35; b, *Diopatra aciculata*, setiger 35; c, *Onuphis eremita*, setiger 85; d, *Hirsutonuphis mariahirsuta*, setiger 35; e, *Nothria conchylega*, setiger 20; f, *Hyalinoecia* nr. *tubicola*, setiger 32.

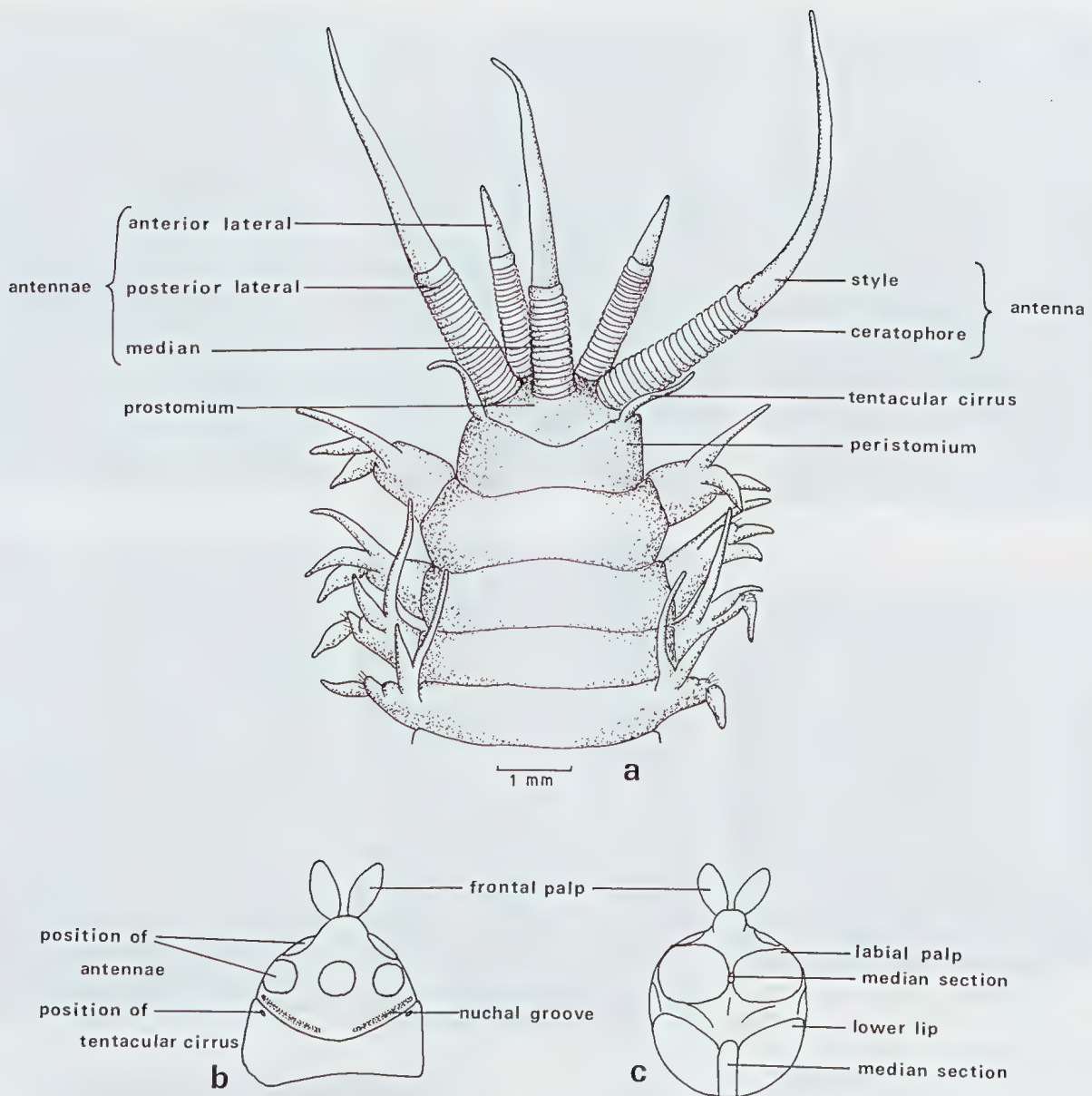


Fig. 3. *Onuphis eremita* (BMNH ZK 1928.4.26.290): a, anterior end, dorsal view; b, stylized diagram of prostomium and peristomium, dorsal view; c, same, ventral view.

(Fig. 4e) or a complete circle around the ciliated area (Fig. 4f). In some species the sensory buds are located on little papilla-like protruberances (Fig. 5a,b). The pattern of distribution of these 'papillae' was used by Hartman (1944) as a taxonomic character and described for a number of species. The configuration and arrangement of the sensory buds appear to be species-specific in *Diopatra* and are being utilized in a forthcoming revision of the genus (Paxton, in preparation).

Palps. The FRONTAL PALPS were referred to as antennae until von Haffner (1959) histologically demonstrated that they are palps and hypothesized that they evolved by a subdivision of the labial palps. Frontal palps are generally present, but reduced to absent in *Neonuphis* and *Leptoecia*. The frontal palps are short, inflated and range in shape from round (Fig. 27a) to oval (Fig. 30a) to subulate or subtriangular (Fig. 23a). The two frontal palps may be close together (Fig. 27a)

or slightly separated (Fig. 34a).

The LABIAL PALPS are oval to rectangular, and can be medially separated (Fig. 34b) or touching (Fig. 30b). A more glandular distal area may be slightly set off (Fig. 34b) or form a distinct distal lobe (Fig. 28b). The area between the palps may be free (Fig. 17b) or folds may outline a 'median section'. This median section may be anterior, i.e. close to the frontal palps (Fig. 27b), or it may be in the centre between the two labial palps (Fig. 3c).

Eyes. Eyes, when present, are situated between the bases of the anterior and posterior lateral antennae. They range from small pigment spots (Fig. 33a) that can be found in some members of most genera, to large eyes with lenses (Fig. 17a). The juvenile anterior eyespots are retained in the adults of some small species.

Nuchal organs. The nuchal organs are chemoreceptors (Mill, 1978) located at the posterior part of the prostomium in the form of ciliated grooves. In

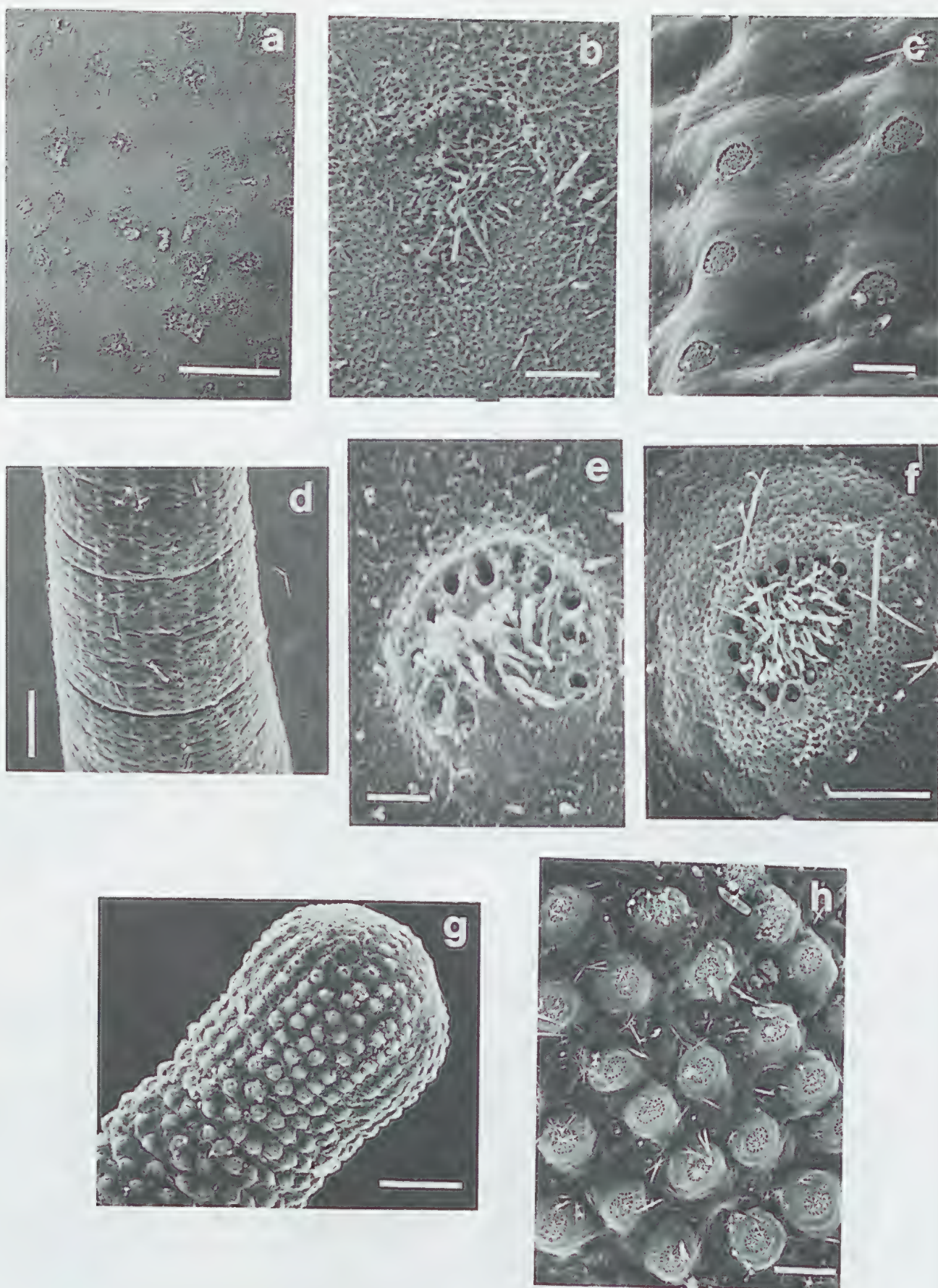


Fig. 4. Scanning electron micrographs of antennae: **a**, irregularly scattered sensory buds of *Hirsutonuphis mariahirsuta* (scale 50 μm); **b**, enlarged sensory bud of same (scale 5 μm); **c**, rows of sensory buds of *Diopatra ornata* (scale 10 μm); **d**, same of *D. cuprea* (scale 100 μm); **e**, enlarged sensory bud of *D. cuprea* (scale 2 μm); **f**, same of *D. dentata* (scale 5 μm); **g**, tip of antenna of *Diopatra dentata* showing sensory buds on papilla-like protruberances (scale 100 μm); **h**, same, enlarged (scale 20 μm).

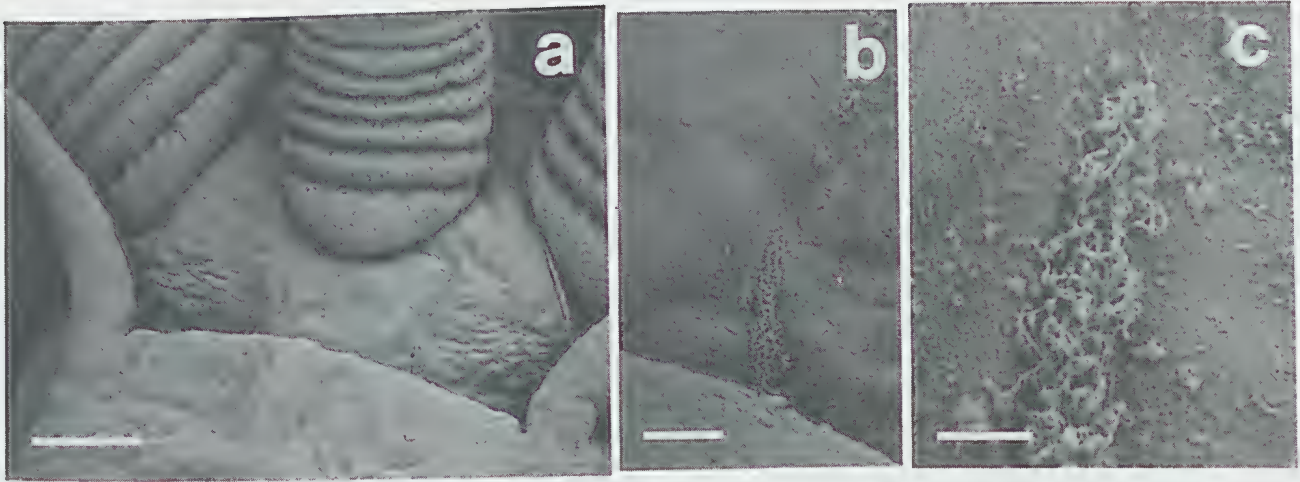


Fig. 5. Scanning electron micrographs of nuchal grooves: a, prostomium and peristomium of *D. n. sp. 1* showing nuchal groove (scale 100 μm); b, same, enlarged (scale 20 μm); c, nuchal groove of same, enlarged (scale 5 μm).

Hyalinoecia tubicola they are associated with the hindbrain in a way similar to that reported for *Eunice* (von Haffner, 1959), as they probably are in all onuphids. The ciliated grooves can be recognized as such in SEM preparations (Fig. 5a-c) and are visible with light microscopy since they stand out as dull bands in the otherwise shiny cuticle (Fig. 3b). The grooves generally run from the position of the eyes (between the anterior and posterior lateral antennae) along the anterior fold of the peristomium and meet middorsally. The grooves may be almost straight and come close together so as to have a small (Fig. 28a) or wide middorsal separation (Fig. 26a), or have a wide separation and curve anteriorly towards the base of the median antenna (Fig. 30a). In species of *Epidiopatra* (Fig. 24a) and *Diopatra* (Fig. 23a) the grooves are short and the lateral and median parts of the grooves are curved anteriorly, forming an arc between and posterior to the median and lateral antenna in the former and almost a circle in the latter genus. This form of nuchal groove was often mistaken for eyes (Hartman, 1944).

Peristomium

The apodous peristomium forms a complete ring. It is dorsally entire in all genera except *Heptaceras* (Fig. 36a) where it has a middorsal notch, and a median raised ridge runs from the peristomium to the median antenna. The peristomium ranges from short (Fig. 19a) to moderately long in most genera (Fig. 3a). The dorsal anterior fold in *Americonuphis* (Fig. 28a) is wrinkled and expansible, forming a protective collar over the nuchal grooves as in *Eunice*. In most genera, the anterior fold is distinct but does not form a collar, while *Australonuphis* (Fig. 30a), *Hartmanonuphis* and *Hirsutonuphis* lack an anterior fold and the peristomium appears to extend middorsally towards the median antenna along the curved nuchal grooves. Ventrally, the peristomium forms a large semilunar to triangular lower lip. A distinct median section (Fig. 3c) is present in many genera but absent in others (Fig. 15b). The furrows outlining the median section are formed by a zone without glands in the otherwise glandular lower lip (Eulenstein, 1914).

Tentacular cirri. Tentacular cirri, when present, occur dorsally on the peristomium. In *Americonuphis* (Fig. 28a) they are situated in the middle of the peristomium, in some genera subdistally (Fig. 15a), while in most genera they emerge distally at the anterior margin of the peristomium.

Parapodia

Polychaete parapodia are typically biramous, consisting of noto- and neuropodia. In the Onuphidae the notopodia are reduced, represented only by the base of the branchiae and the dorsal cirri, thus being subbiramous.

Within the Eunicidae, all segments are rather similar with respect to their length, parapodia and setae. In the Onuphidae, however, the anterior one to eight pairs of parapodia are different from the subsequent ones in their orientation, length, parapodial lobes and types of setae. These anterior parapodia are here referred to as 'modified' to mark their distinction from the subsequent 'unmodified' ones. In genera with a smaller number (2-3) of more highly modified setigers (e.g. *Nothria*, *Rhamphobranchium*) the change is more abrupt than in genera with a larger number (5-7) of less modified setigers (e.g. *Kinbergonuphis*). Hence, it is hard to establish the exact number of modified parapodia in some genera or species since the modifications become gradually less. Therefore, the number of modified parapodia is here defined as the number of parapodia in which the lower setae consist predominantly of hooks.

In many genera, the modified parapodia are directed anteroventrally, ranging from slightly so (Fig. 21c), to moderately (Fig. 1a), to almost touching midventrally (Fig. 29a). As a result of this rotation, the morphologically anterior surfaces are facing each other (Fauchald, 1982a). In another group of genera, the modified parapodia are directed anterolaterally to -dorsally (Fig. 1b), reaching their maximum development in the beachworms (Fig. 32j). The orientation of the last modified or early unmodified parapodia changes gradually, giving the unmodified parapodia a lateral to dorsolateral orientation. The modified parapodia are of about the same length as the

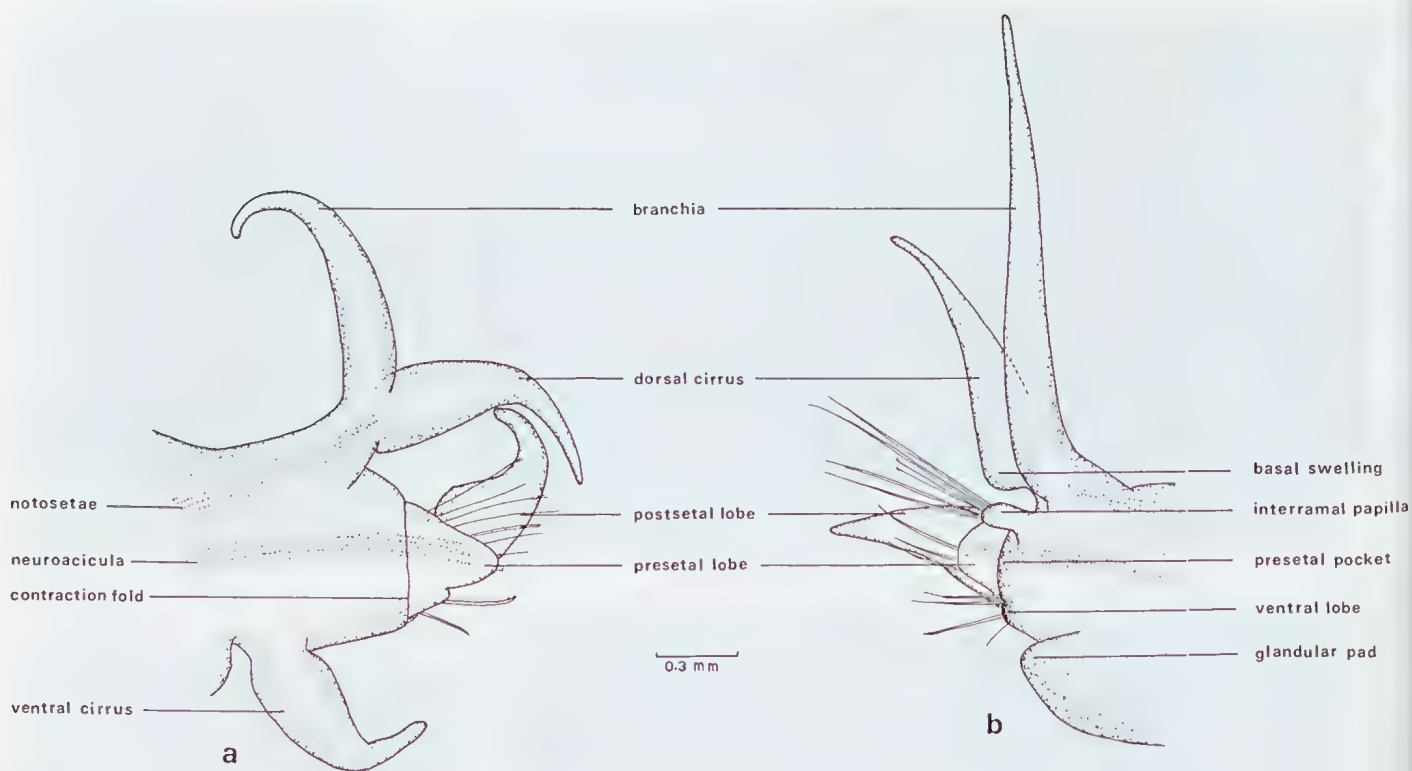


Fig. 6. *Onuphis eremita* (BMNH ZK 1928.4.26.290): a, parapodium 1, anterior view; b, parapodium 8, same view.

median ones (Fig. 3a) or are prolonged. The prolongation ranges from slight (Fig. 34m) to moderate (Fig. 30c) to great (*Longibrachium*). When the parapodia are prolonged, often the first is the longest, or the first three are equally long, and the remaining modified parapodia become gradually shorter. However, in *Australonuphis* and related genera parapodia 2–4 are longest.

The modified parapodia can be extensile, and their length differs with their state of contraction. Contracted parapodia often show furrows or even rings (Fig. 26c). A transverse fold, often present below the presetal lobe, referred to earlier by Fauchald (1968) as a 'low transverse fold', was subsequently designated a 'contraction fold' since it is not a structural feature but can be present or absent depending on the state of contraction (Fauchald, 1980). In the modified parapodia the contraction fold (Fig. 6a) remains as such or can at times be totally extended leaving no fold. However, with the beginning of the unmodified setigers this fold becomes a fixed, often glandular structure (*Rhamphobrachium*, *Australonuphis*) and will be referred to as a presetal pocket (Fig. 6b).

Prolonged modified parapodia are usually also thicker and stouter because of better developed muscles. However, the first segments are generally not much longer, except in *Hyalinoecia* and allied genera, where especially setiger 1 is considerably longer than the following setigers.

Parapodial cirri. The anterior parapodia bear subulate or digitiform VENTRAL CIRRI (Fig. 6a) which are replaced in median and posterior parapodia by ventral glandular pads (Fig. 6b). The number of setigers

with ventral cirri usually agrees with the number of modified setigers. The transition zone between ventral cirri and glandular pads may be short and consists of one or two setigers with globular ventral cirri (*Onuphis*) or glandular pads with reduced cirri (*Hirsutonuphis*). However, species of *Australonuphis* and *Hartmanonuphis* (Fig. 31d) have a long transition zone of glandular pads with reduced cirri (until setigers 14–25), similar to the condition in the Eunicidae.

DORSAL CIRRI are usually present on all setigers and bear internal setae. However, in *Hyalinoecia* and allied genera these cirri lack setae and are posteriorly reduced or absent. Dorsal cirri are usually best developed in the modified parapodia, where they are often of subulate shape and long; these cirri reach their greatest development in the genus *Hirsutonuphis* (Fig. 32j), where in *H. gygis* they approximate the antennae in thickness and length. The dorsal cirri often have a basal swelling (Fig. 6b), which is elaborated into a digital process in some genera (Fig. 30e).

Parapodial lobes. The parapodial lobes consist of acicular, presetal and postsetal lobes and are recognized as such by most authors.

The ACICULAR LOBE is distally truncate or rounded, supported by internal acicula which emerge from its tip.

The PRESETAL LOBE is anterior to the acicular lobe. It is found in all genera, except in the highly modified anterior parapodia of *Rhamphobrachium* and allied genera. In some genera the presetal lobe is very short and follows the outline of the acicular lobe closely, making the two lobes almost indistinguishable. Day (1960) referred to this apparently single lobe in *Diopatra* as the 'setigerous lobe' and stated that the presetal lobe

is not developed in the anterior four parapodia. This terminology was followed by Knox & Hicks (1973) but is not followed here. The presetal lobe can have a moderately large, free distal end (Fig. 36c), or form a hood-like, auricular lobe over the setae as in *Hyalinoecia* and its allies. While the presetal lobes are usually rounded, they may be bilobed (Fig. 23c), trilobed (Fig. 32c), or have a distal extension (Fig. 28b).

The presetal lobes become reduced after the modified parapodia, and the original presetal lobes disappear by setiger 10 to 30. In most species they remain lost, but in a number of larger species they become replaced by the new presetal lips which can be formed in two different ways: (1) In some species of *Onuphis* (Fig. 6b), *Australonuphis* and *Hirsutonuphis* an interrampal papilla appears at the base of the dorsal cirrus immediately after the modified region. In the latter two genera this papilla enlarges ventrally, fuses with the presetal pocket and thus forms a new presetal lip. *Onuphis eremita* develops in addition to the interrampal papilla a small ventral lobe, the two of which fuse and form the presetal lip. (2) In species of *Hartmanonuphis* (Fig. 31d), *Americonuphis* and *Diopatra*, a ventral lobe appears in the early unmodified parapodia, increases dorsally and becomes the new presetal lip. This structure was referred to by Day (1960) as the 'true presetal lobe', and is termed here 'new presetal lip' following Rozbaczylo & Castilla (1981).

The highly modified anterior parapodia of *Rhamphobranchium* and *Longibrachium* lack presetal lobes. However, separate papillae-like lobes are present at the point of emergence of each of the enlarged hooks and are referred to here as papilliform lobes.

POSTSETAL LOBES (Fig. 6) are usually single, of triangular shape with a flattened base and a subulate to digitate distal part. In some species of *Diopatra* and *Brevibrachium* (Fig. 25b) they are double, consisting of a larger upper and a smaller lower accessory lobe. In *Rhamphobranchium* and *Longibrachium* the postsetal lobe is in a more ventral position than in other onuphids and it is likely that it represents the lower part of the double lobe, while the upper lobe has been lost. In juvenile *R. ehlersi* the lower postsetal lobe develops when the parapodium becomes modified (see p. 18), suggesting a separate origin from the usual one. Postsetal lobes are best developed in the modified region, becoming reduced thereafter. In some species, the absence of the postsetal lobes is correlated with the origin of the subacicular hooks (*Rhamphobranchium*), while in others the reduced lobes are continued to the end of the body.

Branchiae. Branchiae are present in the majority of species and occur as outgrowths of the dorsal cirri. The branchiae can be simple, branched, pectinate or spiralled. Simple branchiae (Fig. 17d) are present in small to moderately sized species. The single filaments are often long (overlapping middorsally), and relatively wide and flat. This type has been referred to as 'simple strap-like branchiae' (Fauchald, 1968) and may differ morphologically from others. (Fauchald, 1982a).

Dichotomously branched branchiae have been found only in two species of *Anchinotiria* (Fig. 16d). The most common type are pectinate branchiae. They originate usually as single filaments (Fig. 6) in the anterior body region, and usually rapidly increase their number of filaments by the addition of new ones to the distal part of the main stem (Fig. 7). Spiralled branchiae (filaments attached spirally around the central trunk) are only found in *Diopatra* (Fig. 23d) and *Epidiopatra* (Fig. 24d).

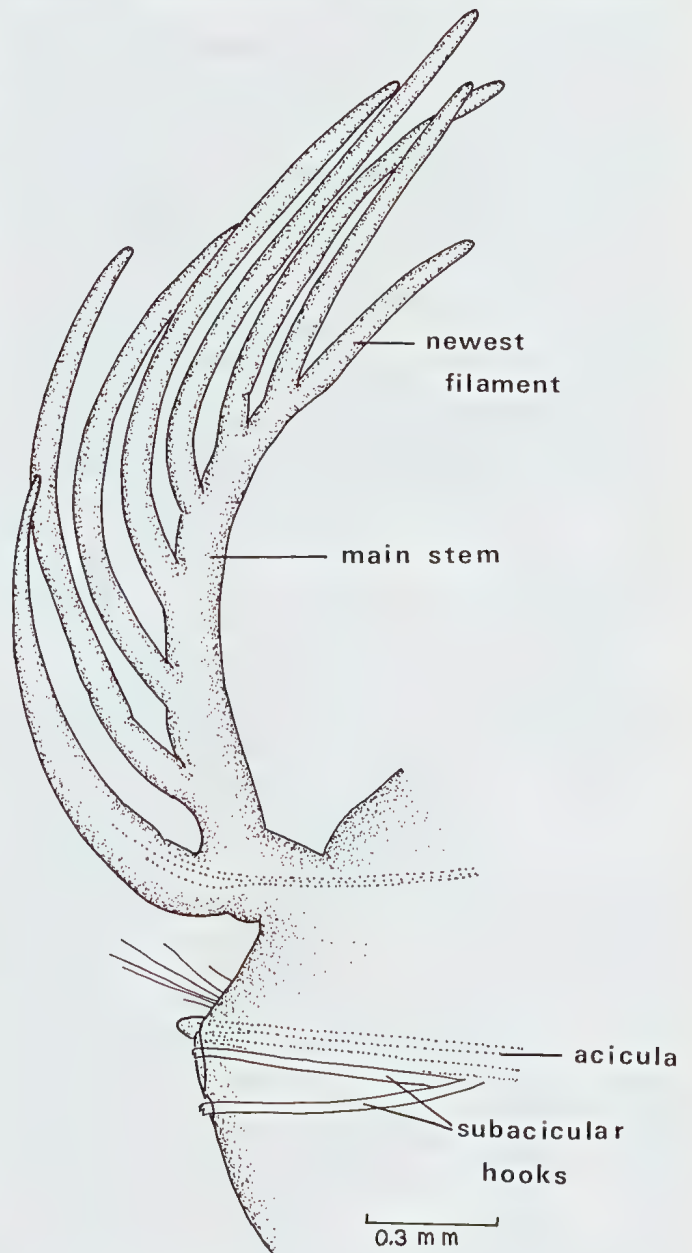


Fig. 7. *Onuphis eremita* (BMNH ZK 1928.4.26.290): parapodium 53, anterior view.

Branchiae may be present from the first setiger or later; in many shallow-water species they start on or about the sixth setiger, while in deep-water ones they often occur after the tenth. In *Diopatra* and related genera the branchiae are well developed in the anterior part of the body and restricted to single filaments from setiger 40–60.

Setae

In the Onuphidae the notosetae are reduced to internal setae in the dorsal cirrus or absent. When present, they are usually short in the modified parapodia (Fig. 6) and longer in the median and posterior region (Fig. 7).

The neurosetae are anchored to the acicula, which number from one to about five. Newly emerged acicula have a filiform tip which may be retained (Fig. 25g) or more commonly, break off, leaving a bluntly rounded tip. In some species the tip projects at an angle (*Diopatra*). The setae of the median and posterior region project dorsolaterally in most genera (Fig. 2a-d,f). However, species of *Nothria* and *Anchinotiria* have ventrolaterally directed setae (Fig. 2e). The setae generally consist of an upper bundle, dorsal and posterior to the acicula, and a lower bundle, ventral and anterior to the acicula. The setal sac is usually contained within the segment from which it originates, except species of the *Rhamphobrachium* complex where the setal sac projects into the following or subsequent segments. The most extreme degree of development of this arrangement occurs in *Longibrachium* and *Rhamphobrachium* where the setal sacs extend to setiger 50–70, where they lie in the body cavity next to the gut and slide anteriorly and posteriorly depending on the

state of extension or retraction. These long setal sacs were thought by McIntosh (1910) to be secreted fibres; Hoagland (1920) recognized them as retractor muscles with attached hooks, and Berkeley & Berkeley (1938) gave a detailed description of the setal sacs.

Upper bundle of setae. The upper bundle of setae consists of simple limbate and pectinate setae.

The UPPER LIMBATE SETAE (Fig. 8a) are long, with narrow wings, often appearing as capillaries. In some species of *Rhamphobrachium*, *Neonuphis* and *Leptoecia* (Fig. 18f) they are densely covered with spines, giving them a spiky or hairy appearance. The upper limbate setae are generally present from the first setiger. However, in *Rhamphobrachium* and *Hyalinoecia* and their respective allies, they do not emerge from the modified parapodia, but are internal supports.

PECTINATE SETAE occur in many genera from the first setiger onwards and throughout the body. The distal pectinate edge may be at either a right angle (transverse) (Fig. 30g) or an oblique angle (Fig. 8c) with the shaft of the seta. The comb of the seta is usually flat, but may be rolled up in anterior parapodia (Fig. 32k). In *Nothria* (Fig. 15l) and *Anchinotiria* the lateral distal parts of the seta are flared towards each other

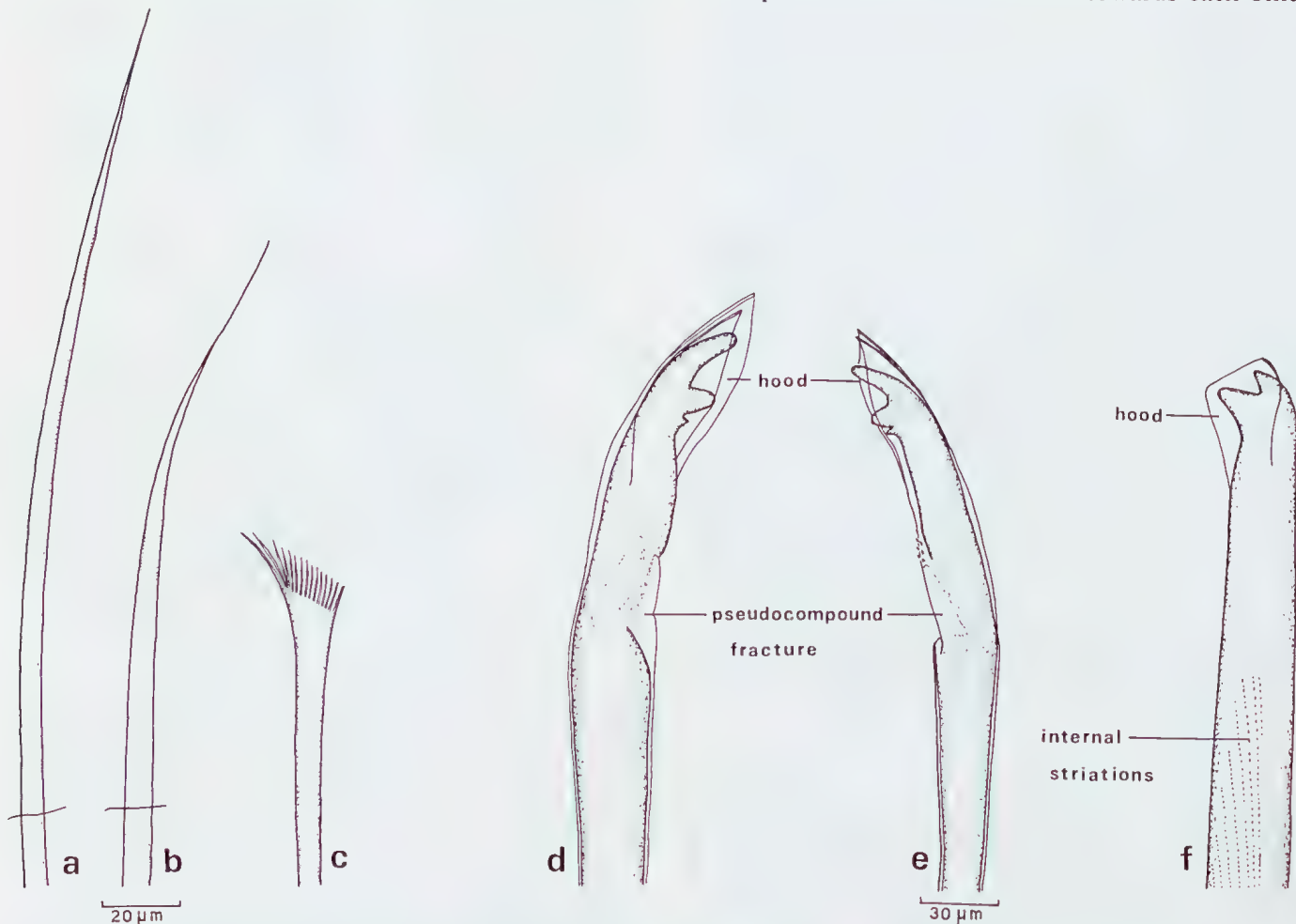


Fig. 8. *Onuphis eremita* (BMNH ZK 1928.4.26.290): a, upper limbate seta from setiger 4; b, lower limbate seta from same; c, pectinate seta from setiger 3; d, median pseudocompound hook from setiger 3; e, lower pseudocompound hook from same; f, subacicular hook from posterior setiger.

forming an 'open scoop', and are termed 'scoop-shaped' (Fauchald, 1982a). Pectinate setae are very numerous in *Hyalinoecia* and allied genera, while their number can vary greatly in other genera.

The number of teeth on pectinate setae was at times considered a good taxonomic character and was used particularly to separate species of *Diopatra* (see Hartman, 1944: 51 for a review). When the number of teeth is low (less than 10) it seems to be a good character, since it aligns *Diopatra neapolitana* and a group of species which also share a number of other features. However, when the number is large (15–30), the variation can be more than 10 teeth in a single specimen so that the number is of little taxonomic value.

Lower bundle of setae. The lower bundle of setae consists typically of hooded bi- to tridentate pseudocompound hooks in the modified parapodia, followed in the unmodified parapodia by short, simple to pseudocompound limbate setae which may remain throughout or become replaced by hooded subacicular hooks. A number of modifications to this basic plan are found and discussed below.

The HOOKS range from pseudocompound to simple. In the majority of species the hooks are pseudocompound; the fracture is completely ankylosed but visible (Fig. 8d,e), or is represented by a clear area (Fig. 23e,j,l). In some species the shaft of the hook shows no sign of fracture, and appears as simple (Fig. 15d,e).

The appendage, or distal part of the anterior hooks can be unidentate (falcate), bidentate or tridentate. The unidentate hooks are found in a number of genera (Fig. 30f). Several authors have considered unidentate hooks as worn bi- or tridentate hooks (e.g. Fauchald, 1982a). However, setae are continually replaced and unidentate replacement hooks are found (Fig. 15c). If the teeth had been lost through wear, certainly the delicate hoods would be lost also, which is not the case (Fig. 15f). unidentate hooks have the distal falcate end and an additional lower second tooth which may be smaller (Fig. 23e), equal in size (Fig. 29c), or thicker (Fig. 36i,j) than the distal tooth. In the tridentate condition (Fig. 8d,e), a usually smaller tooth is present below the second one.

The distal end of the hook is generally covered by a pair of valve-like hoods which range from short and closely fitting (Fig. 8d,e) to long and pointed (Fig. 22c,d).

One or two slightly thicker median hooks (Fig. 8d), located immediately below the acicula, are present in a number of genera from setiger 1. In *Kinbergonuphis* and *Mooreonuphis* (Fig. 35e) these hooks differ from others further in having a more distal pseudoarticulation, and in the shape and orientation of their teeth: the distal tooth is shorter, and the median and lower teeth are blunter and point downwards. They have been referred to as 'precursors of simple tridentate hooks' (Paxton, 1979). The pseudocompound fracture usually becomes weaker and moves more distally in the following segments, and by setiger 3–7 the hook is

simple (Fig. 35g). These large median hooks often remain until the occurrence of the subacicular hooks. The larger hooks were termed 'acicular hooks' or 'tridentate simple hooks' (Hartman, 1944), and 'large hooks' (Fauchald, 1982a). The latter term is modified here to 'large median hooks', and also includes the precursors.

The most modified anterior hooks are found in *Rhamphobrachium* and allied genera. Two species of *Brevibrachium* have regular, hooded uni- to tridentate hooks but the hooks of *B. maculatum* and all species of *Longibrachium* and *Rhamphobrachium* (Fig. 27d,e) have strongly recurved or scythe-like distal ends.

The shafts of hooks have a smooth surface in most genera; in *Rhamphobrachium* and allies they have rows of spines. However, the shafts that appear smooth when viewed with light microscopy show small, irregularly distributed spines in SEM preparations (Fig. 9a). In some species of *Diopatra* (Fig. 9b), some of these spines have lengthened and become oriented into two rows. These rows of spines are well developed in some *Brevibrachium*, *Longibrachium* (Fig. 9c,d), and particularly in *Rhamphobrachium*, where they are moveable (Fig. 9e,f).

The beginning of the unmodified parapodia is marked by the replacement of hooks by LOWER SIMPLE LIMBATE SETAE (Fig. 8b) that are wider and shorter than the upper ones, and may be cultriform (Fig. 23g) to spine-like (Fig. 24g). In some genera the lower limbate setae are weakly pseudocompound to compound (i.e. spiniger) (Fig. 35h). The lower limbate setae are present throughout the median and posterior region in *Hyalinoecia* (Fig. 17d) and allied genera. However, in *Onuphis* (Fig. 7) and related genera, the lower limbate setae are absent after the appearance of subacicular hooks.

Some species of *Rhamphobrachium* also have COMPOUND FALCIGERS, strongly reminiscent of eunicid falcigers in the first two unmodified pairs of parapodia.

SUBACICULAR HOOKS occur in all onuphids examined and start from setiger 8 to 80. They occur either in a ventral or median position in the fascicle. Fauchald (1982a) restricted the term 'subacicular hooks' to the former, and referred to the latter as 'intrafascicular hooks'. However, since the two types appear to be homologous and both occur in a subacicular position, it is recommended that the established name be retained for both types.

Both types of subacicular hooks are simple and show clear internal striations. Both types are hooded and bidentate (Fig. 8f), except in *Australonuphis* (Fig. 30j) where the hooks are distally entire and lack a hood. In most genera they number two per parapodium from their origin and continue as such. In *Hyalinoecia* they originate as one per parapodium, increase to two, and rarely three, after several segments. A similar pattern occurs in *Rhamphobrachium*, while in two species of this genus they increase to a maximum of three to six, and then decrease to the typical two per parapodium, which is then retained.

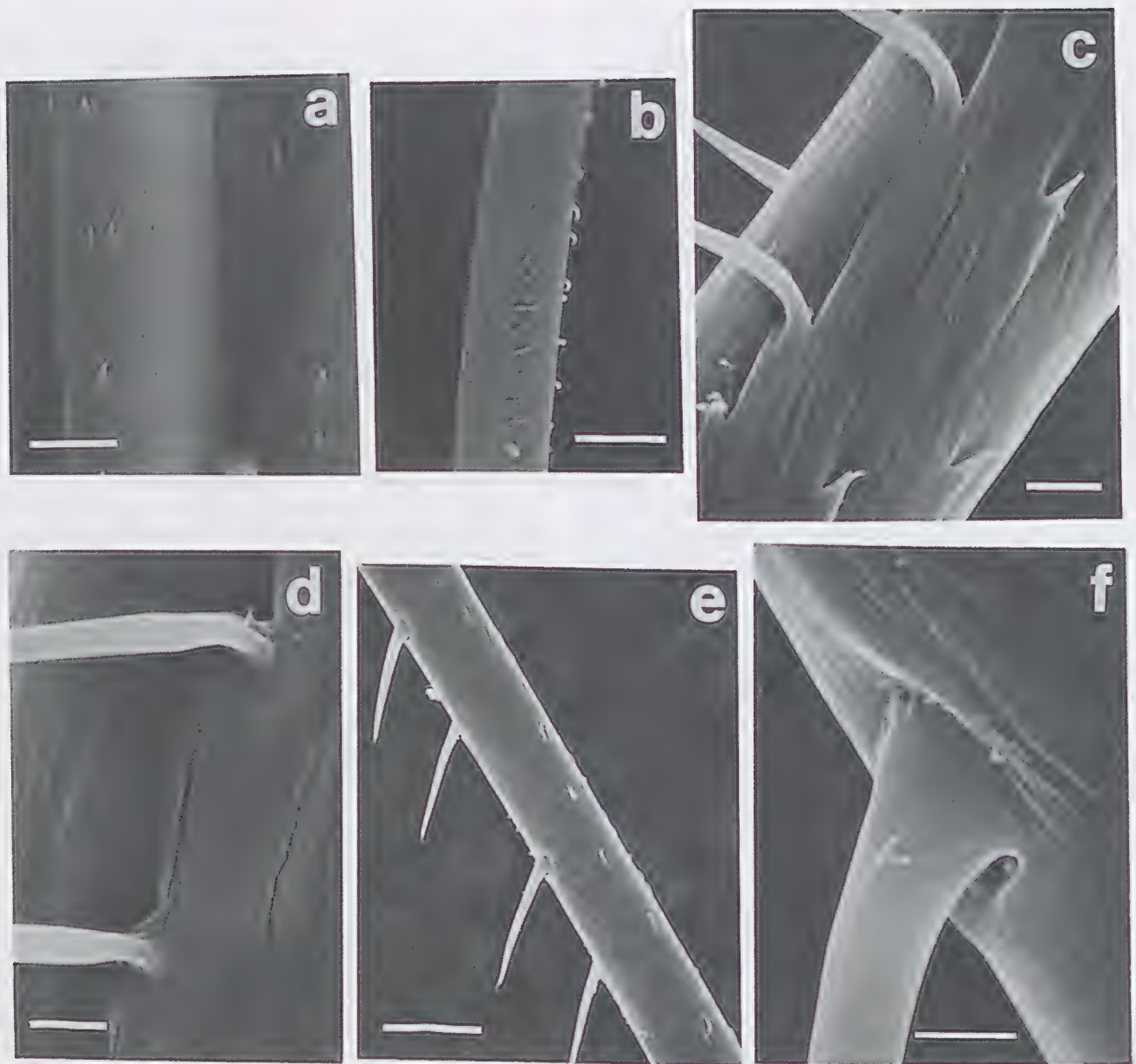


Fig. 9. Scanning electron micrographs of setal hooks: a, shafts of *Brevibrachium maculatum* (scale 5 μ m); b, shaft of *Diopatra* n. sp. 1 (scale 5 μ m); c, shaft of small hook of *Longibrachium longipes* (scale 2 μ m); d, shaft of large hook of same (scale 2 μ m); e, shaft of *R. (Rhamphobranchium) longisetosum* (scale 20 μ m); f, same enlarged (scale 2 μ m).

Ventral subacicular hooks occur in most genera. The upper subacicular hook runs parallel to the lowest aciculum, while the lower subacicular hook originates at, or slightly above, the acicula, emerging usually considerably lower, thus forming an acute angle to the upper subacicular hook and the acicula (Fig. 7). Lower limbate setae are absent from the start of the subacicular hooks, and the latter are now the most ventral setae in the fascicle. As was noted by Fauchald (1982a), the ventral subacicular hooks are round in transverse section, and usually barely emerge from their setal sacs.

Median subacicular hooks are found in *Hyalinoecia* (Fig. 17d) and related genera. They originate just below the acicula and follow it closely, emerging parallel to it in the middle of the parapodium. The median subacicular hooks do not replace the lower limbate setae, which continue ventrally to the subacicular hooks

until the end of the body. The median subacicular hooks are oval in transverse section (Fauchald, 1982a) and emerge much further from their setal sacs than the ventral hooks.

Eversible Pharynx

The eversible onuphid pharynx is a ventral structure projecting backwards under the oesophagus as a muscular sac (Dales, 1962). A detailed study of the eversible pharynx of *Hyalinoecia tubicola* was made by von Haffner (1959). The eversible pharynx contains an elaborate jaw apparatus consisting of a pair of ventral mandibles and 4½ to 5½ pairs of dorsal maxillae.

Mandibles. The mandibles (Fig. 10a) are solid structures consisting of long shafts widening into anterior cutting plates which are connected to each other

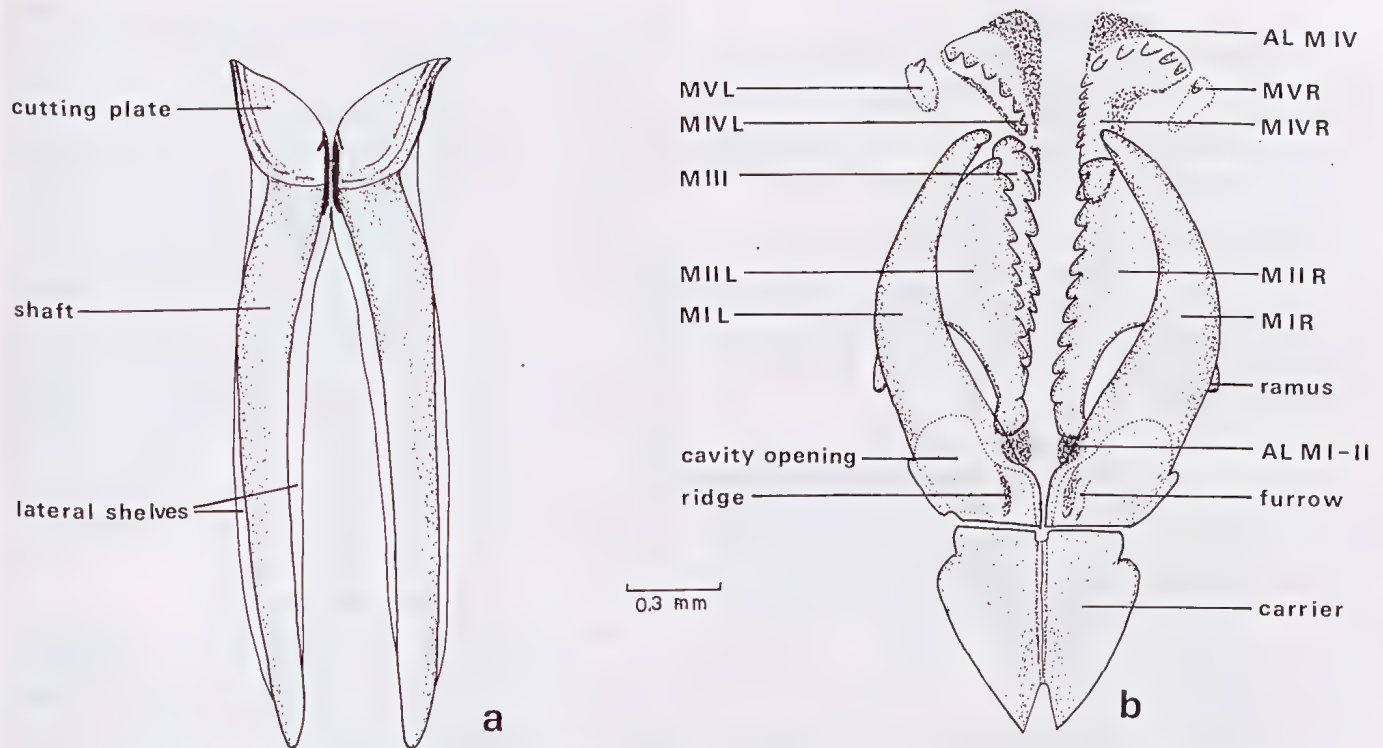


Fig. 10. *Onuphis eremita* (BMNH ZK 1928.4.26.290): a, mandibles, decalcified, ventral view; b, maxillary apparatus, dorsal view (AL = attachment lamella, L = left; M = maxilla; R = right).

by a ligament. The length of the mandibles equals, in most genera, the length of the maxillary carrier and maxilla I together. However, in some groups the mandibles seem disproportionately large (Fig. 15m). The shafts are centrally thickened and often have distinctly thinner lateral shelves. The cutting plates consist of a sclerotized dorsal matrix and a thick, ventral layer of calcium carbonate that is usually twice as long as the matrix and often anteriorly serrated (Fig. 24i).

Maxillary apparatus. The maxillary apparatuses (Fig. 10b) range from the most delicate, translucent, hardly sclerotized or calcified structures of small species (Fig. 19h) to the robust, opaque, highly sclerotized and calcified structures of large species (Fig. 23k). The apparatus is made up of a pair of medially hinged posterior carriers and anterior maxillae. The hardened part of the maxilla provides an exoskeleton for the soft structure of the pharynx through basal cavity openings. The latter range from relatively small (Fig. 10b) to very large (Fig. 19h). The maxillae (abbreviated as Mx) are conventionally enumerated in Roman numerals in an anterior direction. Maxillae I, II and IV are each paired, while III is a single left plate. The right Mx IV is larger than the left Mx III and was considered a fused right Mx III and Mx IV by Hartman (1944), and followed by Day (1967) and Fauchald (1968). However, as pointed out by Kielan-Jaworowska (1966), while there is no support for this interpretation from Recent material, it is contradicted by fossil evidence.

The numbers of median teeth on the maxillary plates are described by the dental formula, where the numerals represent the number of teeth on the respective left and

right maxillary plates. The dental formula for *Onuphis eremita* (Fig. 10b) is thus represented as follows: Mx I = 1 + 1; Mx II = 9 + 9; Mx III = 8 + 0; Mx IV = 6 + 12; Mx V = 1 + 1. The absence of a plate is indicated by a zero, e.g. 'Mx III = 8 + 0' states that the left Mx III has 8 teeth, while the right Mx III is absent.

The maxillae I (or forceps) are attached to the carriers by hinges. Proximally, the left Mx I has a ridge which fits into the corresponding furrow of the right Mx I, interlocking like a 'Druckknopf' (Hartmann-Schröder, 1967) or snap. This basal ridge is interpreted as the remnant of the laeobasal plate in fossil eunicids (Kielan-Jaworowska, 1966). The lateral ramus of the Mx II is usually covered by the Mx I but is protruding in some genera (Fig. 10b). The Mx II are attached posteriorly to the Mx I by an often darkly sclerotized attachment lamella. The more anterior maxillae are usually free from each other. The Mx III may originate posteriorly at the same level as Mx II (Fig. 17l), or more anteriorly (Fig. 31i). It is usually longer anteriorly than Mx II (Fig. 10b), except in *Nothria* (Fig. 15n) and *Anchinotiria* (Fig. 16k). The distal tooth of Mx II is sometimes enlarged, forming a fang (Fig. 16k).

The Mx IV are disproportionately large in some groups (Fig. 19h). The attachment lamellae of the Mx IV (Fig. 10b) have been elaborated into large sclerotized areas that were also termed 'Schwielen' (Heider, 1925) or 'callosités' (Desière, 1967). Mx V are small plates having one tooth each. They can be very small (Fig. 10b) or larger (Fig. 23k); Mx VI are present in some genera as toothless plates (Fig. 27l), or even bear a small tooth each (Fig. 28d), but are absent in most genera.

Pygidium

The pygidium is generally a small lobe with a dorsal anus, while in *Hyalinoecia* it consists of an enlarged glandular structure. The pygidium bears anal cirri which are a single pair in *Hyalinoecia* and allies (Fig. 15j), while in other genera there is a larger ventral and smaller dorsal pair.

Kinbergonuphis pygidialis (Fauchald, 1968) was described as having a single anal cirrus with a bifid tip. I have not observed any other specimens with only one anal cirrus and presume that the single specimen upon which the description was based, was aberrant or damaged in this respect.

Tubes

The tubes are generally round in transverse section and longer than their inhabitants. Flattened tubes occur in *Nothria*, *Neonuphis* and *Leptoecia*. The tubes usually consist of an inner lining secreted by its inhabitant, and an outer layer of foreign particles. The internal lining of *Diopatra* and other genera consists of a tough, parchment-like material, while that of *Onuphis* and others consists of a softer mucous substance which is extremely fragile in some groups. Only rarely is the outer layer absent as in the quill-like tubes of *Hyalinoecia*. The chemical composition of the *Hyalinoecia* tubes was found to be a combination of onuphic acid and a mucoprotein (Defretin, 1971). *Hyalinoecia* tubes are also unique in having internal valves.

The outer layer of the tube consists of sand grains, fragments of hard parts from other animals, or plants. Fauchald (1982a) stated that some selection of particles apparently takes place since the particles attached to the tube are usually larger than the mean particle size in the surrounding medium.

Size

Species of *Nothria* are short-bodied, measuring up to 5 cm for less than 100 setigers, even though their width can attain up to 6 mm. Most onuphids have a length of about 10 cm (up to 200 setigers), and a width of up to 3 mm, while species of the *Rhamphobrachium* complex and *Diopatra* can measure up to 30 cm long (up to 250 setigers) and up to 8 mm wide. However, the longest of all onuphids are species of *Americanuphis* and the beachworms, which can attain a length of 70 cm (1000 segments), width of 10 mm, and live specimens can measure up to 300 cm.

REPRODUCTION AND DEVELOPMENT

Knowledge of the reproductive biology of onuphids is scant. Reference to many of the earlier studies can be found in Richards (1967). Additional or newer papers are listed in Table 1. Of the 27 species in the combined listing, accounts for 10 species merely reported the presence of gametes or brooding, while studies of the remaining species dealt with various aspects of reproduction, development and life history. The fact that many species live in great depths and that even

littoral species cannot be collected and kept easily in the laboratory explain the gaps in our understanding of their life history.

Onuphid eggs are relatively large (175 to 1,170 μm in diameter); development is either by lecithotrophic planktonic larvae, direct development with brood care in the parental tube, or viviparity. While the sexes are usually separate without sexual dimorphism, cases of hermaphroditism (Lieber, 1931) and male dwarfism (Hartman, 1967a) have been observed. Very small specimens of the Antarctic *Rhamphobrachium ehlersi* Monro, 1930 observed in the present study contained sperm morulae and free sperm, suggesting that the species is a protandric hermaphrodite. Asexual reproduction has not been reported. The following discussion is limited to aspects of development of features of taxonomic importance and their relevance to intergeneric relationships.

Reproduction

During oogenesis, onuphid oocytes are associated with nurse cells (Schroeder & Hermans, 1975) which occur in two different types of arrangement. In *Onuphis* and other genera the nurse cells are attached to the oocyte as two strings of cells (Fig. 11a), while in *Hyalinoecia* and allies they are attached in a cluster (Fig. 11b). When viewed with light microscopy the primary envelope of mature eggs in the former group appears smooth, while that of the latter group is densely pitted (Bergmann, 1903: pl. 17 figs 17–19).

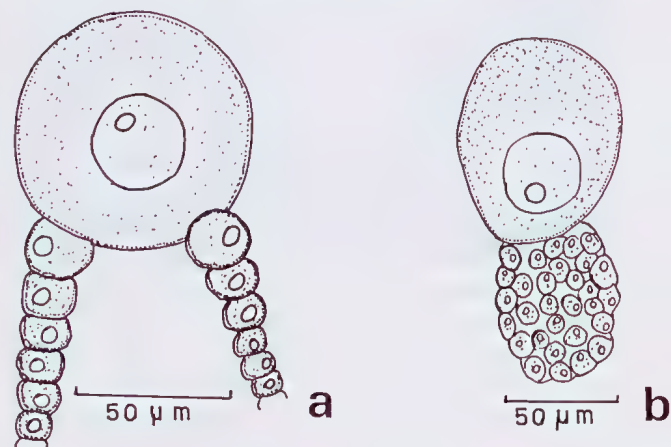


Fig. 11. Oocytes: a, oocyte of *Australonuphis teres* with strings of nurse cells; b, oocyte of *Hyalinoecia tubicola* with cluster of nurse cells.

Fauchald (1983) discussed life diagram patterns in benthic polychaetes and included onuphids of four different genera in the category of perennial species, characterized by: low reproductive effort, moderately large to large eggs, and non-planktotrophic development. The species listed by him have relatively few eggs per spawning (less than 3,200). However, large individuals of the Australian beachworms, *Australonuphis teres* (Ehlers, 1868), examined during the present study contained more than 100,000 eggs in their body cavity, making this one reproductive effort higher than the lifetime investment considered as

Table 1. Summary of Reproduction, Development and Life History Studies in the Family Onuphidae

Species	Location	Observation	Reference
<i>Nothria conchylega</i>	North Sea	Oogenesis.	Eulenstein, 1914
<i>N. nr. conchylega</i>	S. Shetland Islands	Eggs in adult tube.	Hartman, 1967a
<i>Hyalinoecia araucana</i>	Central Chile	45-69 larvae (3-13 setigers) in adult tube.	Carrasco, 1983
<i>H. tubicola</i> (as <i>Onuphis tubicola</i>)	Naples, Italy	Oogenesis.	Bergmann, 1903
<i>H. tubicola</i>	Sweden	Sperm morphology.	Franzén, 1956
<i>Notonuphis antarctica</i> (as <i>Paronuphis antarctica</i>)	Antarctic	Eggs 1.17 mm diameter and up to 24-setiger juveniles in adult tube; pygmy ♂ (4 mm long) firmly appressed to ♀.	Hartman 1967a, b
<i>Diopatra nr. amboinensis</i>	Java	Oogenesis Yellowish-white eggs and up to 6-setiger larvae in adult tubes; eggs singly attached on inside of tube near distal end; juveniles build own tube on outside of parental one.	Lieber, 1931 Pflugfelder, 1929
<i>D. cuprea</i>	North Carolina, U.S.A. Florida, U.S.A.	Artificial fertilization. Eggs 200 µm diameter; 1600-3200 eggs/spawning; 4 spawnings/life of ♀.	Just, 1922 Fauchald, 1983
<i>D. nr. cuprea</i>	Sumatra	Oogenesis.	Lieber, 1931
<i>D. neapolitana</i>	?Naples, Italy	Oogenesis.	Lieber, 1931
<i>D. ornata</i>	S. California, U.S.A.	Eggs 235 µm diameter; 900 eggs/spawning; 4 spawnings/life of ♀.	Fauchald, 1983
<i>D. variabilis</i>	India	Osmoregulation of eggs and larvae.	Krishnamoorthi, 1963
<i>D. n. sp.</i>	Sumatra	♂♂, ♀♀, and hermaphrodites with ♂ and ♀ gonads in the same segments; oogenesis. Three generations of tubes together.	Lieber, 1931 Pflugfelder, 1929
<i>Brevibrachium maculatum</i> (as <i>Rhamphobrachium</i> sp.)	Victoria, Australia	Summer breeding season; eggs 300-500 µm diameter and up to 28-setiger juveniles in lateral chambers of adult tube.	Smith and Jensz, 1958
<i>Americonuphis magna</i> (as <i>Onuphis magna</i>)	North Carolina, U.S.A.	Eggs in gelatinous strings (2 m or more).	Hartman, 1945
<i>Australonuphis teres</i>	Eastern Australia	Eggs light green; 260 µm diameter; 'primitive' sperm.	Paxton, 1979
<i>A. pareteres</i>	Eastern Australia	Eggs cream with green spots; 280 µm diameter; 'primitive' sperm.	Paxton, 1979
<i>Hirsutonuphis mariahirsuta</i> (as <i>Onuphis mariahirsuta</i>)	Eastern Australia	Eggs 240 µm diameter.	Paxton, 1979
<i>Kinbergonuphis notialis</i> (as <i>Nothria notialis</i>)	Antarctic	2-3 eggs and up to 29-setiger juveniles in each of numerous lateral capsules of adult tube.	Hartman, 1967a, b
<i>K. pulchra</i>	Belize, Central America	Eggs 330 µm diameter; 74 eggs/spawning; 3 spawnings/life of ♀; non-planktotrophic.	Fauchald, 1983
<i>K. taeniata</i> (as <i>Onuphis taeniata</i>)	Queensland, Australi	Eggs 240 µm diameter.	Paxton, 1979
<i>K. simoni</i> (as <i>Onuphis simoni</i>)	Florida, U.S.A.	Eggs and up to 20-setiger juveniles in adult tube. Eggs 360 µm diameter; 46 eggs/spawning; 3 spawnings/life of ♀; non-planktotrophic.	Santos <i>et al.</i> , 1981 Fauchald, 1983
<i>Mooreonuphis jonesi</i>	Bermuda	Eggs 175 µm diameter in body cavity; 50-60 up to 10-setiger juveniles in brood chamber of adult tube. 22 eggs/spawning; 3 spawnings/life of ♀.	Fauchald, 1982b Fauchald, 1983
<i>Onuphis elegans</i> (as <i>Nothria elegans</i>)	California, U.S.A.	Eggs 230 µm diameter; 'primitive' sperm; lecithotrophic planktonic larvae; feeding delayed until just prior to settlement at 6 days; artificially fertilized and reared through 60-setiger juveniles. 789 eggs/spawning; 4 spawnings/life of ♀.	Blake, 1975 Fauchald, 1983
<i>Onuphis eremita oculata</i>	Florida, U.S.A.	Eggs 210 µm diameter; 4 spawnings/life of ♀; non-planktotrophic.	Fauchald, 1983

characteristic for perennial species by Fauchald (1983).

The directly developing worm in an egg mass or parental tube, limiting its dispersal, is defined as an embryo, while free-spawned eggs develop into a larva; both types become juveniles when they enter the adult environment (Schroeder & Hermans, 1975).

Juvenile Development

Juveniles in various stages of growth, of many species, were observed. For one species, the Antarctic *Rhamphobrachium ehlersi*, a complete growth series of juveniles together with adult specimens was obtained from a single sample. This fortunate find allowed the elucidation of juvenile *Rhamphobrachium* development, leaving no doubt as to the conspecificity of the various stages. An incomplete series of juveniles of an undetermined species of *Rhamphobrachium* from Australia showed the same basic growth pattern, but some variations in the setal pattern. This section will firstly describe juvenile states of *Rhamphobrachium ehlersi* and *R. sp.*, to be followed by a discussion of general juvenile characters.

The juveniles of *R. ehlersi* can be divided into four stages (Table 2).

Stage 1. Antennae present, ceratophores not ringed. Frontal palps beginning to develop, tentacular cirri absent. Only parapodium 1 prolonged, three

characteristic spiny hooks protruding. Parapodium 2 short with internal spiny hooks, low postsetal lobe starting to develop. Parapodium 3 short with limbate setae. Subacicular hooks present from setiger 6–8, branchiae absent.









Stage 2. Frontal palps present, tentacular cirri ranging from absent to short. Both parapodia 1 and 2 prolonged with protruding spiny hooks. Parapodium 3 short, bearing limbate setae. Subacicular hooks present from setiger 8–10. Single branchial filaments present from setiger 11–13, about the same origin as in adults.

Stage 3. Prostomial parts similar to stage 2. Parapodia 1 and 2 same as in stage 2. Parapodium 3 short, its low postsetal lobe starting to develop. Limbate setae and 1 to 4 compound falcigers present in parapodium 3. Subacicular hooks present from setiger 10–13.

Stage 4. Prostomium and parapodia 1 and 2 as before. Parapodium 3 short, low postsetal lobe has lengthened; ventral falcigers lost, replaced with internal spiny hooks. Subacicular hooks present from setiger 14–16.

Adult. Three pairs of prolonged parapodia with protruding spiny hooks, subacicular hooks start on setiger 15–16. Branchiae start on setiger 10–12 as single filaments, becoming bifid by setiger 20.

Table 2. Ontogenetic changes of *Rhamphobrachium ehlersi*

Character	Stage 1	Stage 2	Stage 3	Stage 4	Adult
Anterior end					
Frontal palps	beginning	present			
Tentacular cirri	absent	absent to short		present	
Parapodium 1					
Setae	protruding spiny hooks				
Parapodium 2		prolonged			
Setae	internal spiny hooks	protruding spiny hooks			
Parapodium 3					prolonged
Setae	limbate		+ falcigers	internal spiny hooks	protruding spiny hooks
Subacicular hooks from set.	7-8	8-10	10-13	14-16	15-16
Branchiae from setiger	absent	11-13	11-14	11-14	10-12
Length (mm); setigers (no.)	12; 31	15; 50	19; 57	15 ⁺ ; 41 ⁺	45; 72
Width (mm)	0.7-1.0	1.0-1.3	0.8-1.3	1.1-1.8	1.8-3.5

Rhamphobrachium sp. Juveniles of stages 1 and 2 range in length from 10–22 mm for 50–100 setigers. Frontal palps, tentacular cirri and branchiae absent in all specimens. Parapodia 1 and 2 range from short to prolonged, with internal to protruding spiny hooks. Parapodium 3 and subsequent ones short with upper limbate setae and 6–8 lower simple bidentate hooks with wings (Fig. 13c). These setae considered as precursors of subacicular hooks, because of their similar shape and position. Wings largest on hooks of setiger 3, becoming gradually smaller in subsequent segments until hooks resemble adult subacicular hooks, becoming reduced to 2 per parapodium by setiger 20–25, retained as such until the last few segments. In terminal 2 to 3 setigers, simple precursor subacicular hooks may be replaced by compound precursor subacicular hooks.

General Juvenile Characters of Onuphidae

Colour pattern. Many shallow-water onuphids have dark brown dorsal pigmentation, the pattern of which spreads in a definite sequence. The most common type is a series of dorsal horizontal bands (Fig. 34m). Initially there are two lateral patches per segment which spread towards the middle and form the band. *Diopatra aciculata* has a more complex pattern which starts with a median anterior patch and two lateral posterior patches on each segment (Fig. 12a). Both groups of patches spread, the anterior one laterally and the lateral ones medially (Fig. 12b), to be followed by a breaking up of the anterior lines into patches (Fig. 12c), the

middle of which is the most distinctive and is usually the only one remaining in adults. Juveniles sometimes have a dark band on the peristomium (Fig. 12a) which is absent in adults.

Antennae. The development of antennae in embryos and larvae has been documented for a number of species, e.g. *Nothria elegans* (= *Kinbergonuphis elegans*; Blake, 1975). In juveniles the ceratophores are smooth, indistinctly ringed, or have less rings than in adults. The styles of young juveniles can be inflated and clavate (*Australonuphis*; Paxton, 1979: figs 59, 60) or subulate (*Hyalinoecia artifex*; Mangum & Rhodes, 1970: fig. 4), later becoming tapered and more slender. Fauchald (1982a) noted that small specimens usually have longer antennae than larger specimens of the same species relative to the total length of the body.

Frontal palps and tentacular cirri. Both sets of structures are absent in young juveniles. Their development is independent; in some species the frontal palps are formed first (Fig. 12), in others the tentacular cirri appear first (*Australonuphis*). Frontal palps appear as two protrusions marked off by a furrow from the labial palps, and then elongate (Paxton, 1979). The tentacular cirri start as lateral outgrowths on the anterior part of the peristomium, and elongate (Fig. 12b,c).

Eyes. A pair of anterior eyespots develops early in larvae (e.g. *Kinbergonuphis elegans*; Blake, 1975) and embryos (e.g. *Diopatra variabilis*; Krishnan, 1936). These eyespots may be followed by another posterior

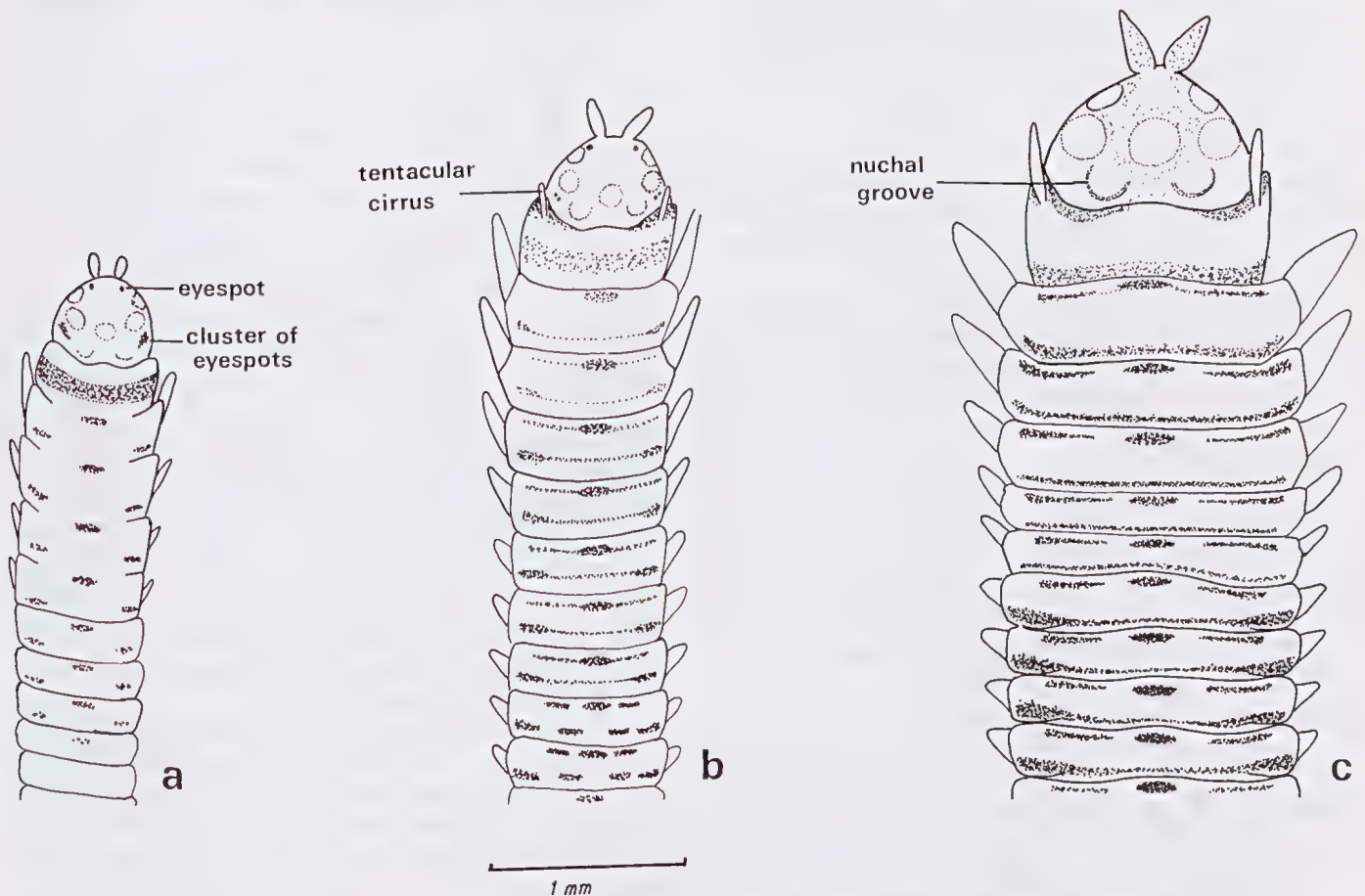


Fig. 12. Juveniles of *Diopatra aciculata* (parapodial detail and branchiae omitted): a, young juvenile; b, juvenile; c, young adult.

pair. The anterior pair is usually distinct while the posterior pair can consist of two clusters of eyespots (Fig. 12a). The anterior eyespots are retained only in the adults of some small species, while they are generally lost; the posterior ones are more often present in adults, but may be lost as well.

Nuchal grooves. Nuchal grooves are straight in small juveniles. They either remain as such (*Onuphis*) or become curved towards the median antenna (Fig. 30a). In species of *Diopatra* (Fig. 12) the grooves curve anteriorly at both ends, developing into a semicircle in small species, or an almost complete circle in large species (Fig. 23a).

Modified anterior parapodia. In *Rhamphobranchium ehlersi* the development of specialized setae precedes the prolongation of the modified parapodia. The number of modified parapodia in juveniles is less than in adults, where it is more or less stable within a species.

Branchiae. Young juveniles may develop ciliated juvenile branchiae on setigers 6–8 soon after the formation of these segments (Blake, 1975; Fauchald, 1982b). The juvenile branchiae may be retained and adult branchiae added, first posteriorly and later anteriorly when the worms are considerably larger, as in *Kinbergonuphis elegans* (Blake, 1975); or the larval branchiae are lost, the juveniles are abbranchiate for a period of time and adult branchiae develop later, as in *Mooreonuphis jonesi* (Fauchald, 1982b). The development of adult branchiae can start as early as in 10-setiger worms (*Diopatra variabilis*; Krishnan, 1936), or not before they reach 50 setigers (*R. ehlersi*) or later. Species with compound branchiae add filaments as they grow, but remain within a certain range of development that is characteristic for the species.

Setae. The setal progression occurring in larvae, embryos and juveniles has been documented for *Diopatra variabilis* (Krishnan, 1936), *D. cuprea* (Allen, 1959), *Kinbergonuphis elegans* (Blake, 1975) and *Hyalinoecia araucana* (Carrasco, 1983).

The setal development in onuphids does not follow a single pattern; considerable differences occur even within one genus as is demonstrated for *R. ehlersi* and *R. sp.* above. Although these processes are not completely understood, an attempt is here made to identify general trends.

The presence of certain types of setae in larvae and juveniles that are absent in adults has been noted by several authors and referred to as 'provisional' setae by Krishnan (1936), as opposed to 'permanent' or adult setae. The provisional setae (Fig. 13) are reminiscent of eunicid setae, indicating their relict nature.

Simple provisional setae have been observed in *Rhamphobranchium sp.* and species of *Diopatra*. In *R. sp.* these consist of bidentate winged hooks (Fig. 13a) (see above). The two species of *Diopatra* studied were reported to have 'pointed setae' (Krishnan, 1936: fig. 12c) or 'curved pointed' (Allen, 1959: pl. V figs 29–32) in parapodium 1 and 'blunt-tipped' (Krishnan, 1936: fig. 12b) or 'short-tipped winged' (Allen, 1959: pl. V

figs 32–34) in parapodia 2 to 4–7 in embryos and larvae. The newly formed posterior segments carry permanent or adult setae and, by the time the juveniles of *Diopatra* consist of 15 setigers, most provisional setae have been replaced by permanent setae. However, the distribution of these permanent setae is different from the adult pattern.

The provisional setae of *K. elegans* and *H. araucana* consist of compound falcigers. While adult-like setae of parapodium 1 also appear in about the 15-setiger juveniles in these two species, the remaining provisional setae are retained longer than in *Diopatra*.

Compound provisional setae (or falcigers) were observed in the present study in juveniles of *Rhamphobranchium*, *Onuphis*, *Kinbergonuphis* and *Hyalinoecia*, and thus appear to be more common than the simple types.

The provisional setae are the precursor setae for the hooks of the modified parapodia and for the subacicular hooks. Permanent or adult hooks are restricted to the first parapodia in young juveniles. From the second parapodia onwards the provisional setae are present until they are replaced by the adult hooks which appear sequentially until the typical number of parapodia with hooks for the particular species is attained. For instance, small juveniles of *K. taeniata* have permanent pseudocompound hooks on setigers 1–3 and provisional compound falcigers on setigers 4–7, while adults of the same species have seven setigers with pseudocompound hooks.

In species of *Rhamphobranchium*, the provisional falcigers are sometimes present for only a short period of time (e.g. *R. ehlersi*, stage 3). Rarely, compound falcigers are retained as a presumably neotenic feature in the first unmodified setigers of adults (e.g. *R. diversosetosum*); however, generally the presence of falcigers in anterior parapodia indicates the juvenile state of the specimen.

The 'large median hooks' characteristic of *Kinbergonuphis* and *Mooreonuphis* are absent in juvenile *K. taeniata*, and presumably in other species as well. These hooks may represent a relatively recent specialization, thus developing late in ontogeny.

Subacicular hooks start as one or two hooks in embryos or small juveniles either from setiger 6–8 in their adult form (*R. ehlersi*, *Diopatra spp.*), or as a provisional form from setiger 2–5 to be replaced by the adult form from about setiger 8. The provisional form is compound in *Onuphis* (Fig. 13a) and *K. elegans* (Blake, 1975: fig. 6c), and simple in *Rhamphobranchium sp.* (Fig. 13c). The anterior permanent subacicular hooks of *Diopatra* are parallel to the acicula and project far from their setal sacs (Fig. 13d).

Compound provisional subacicular hooks in the most posterior setigers of *Hyalinoecia tubicola* were observed a long time ago (Langerhans, 1880; Saint-Joseph, 1906; Eulenstein, 1914) and attributed to the juvenile state of the specimens, a statement that is supported here (Fig. 13e).

The origin of subacicular hooks remains at setiger

8–10 in the adults of a number of species, while in others the origin will move posteriorly until the adult origin is reached. This size dependent variation in the origin of subacicular hooks has been noted previously (Hobson, 1971; Amoureux, 1982; Fauchald, 1982a). In most species the adult origin of subacicular hooks is

constant; however, in *Australonuphis* it continues to be displaced posteriorly, with subacicular hooks starting at setiger 70–80 in very large specimens.

Limbate and pectinate setae were found only in their permanent form. Limbate setae are present early in development, while pectinate setae usually appear later.

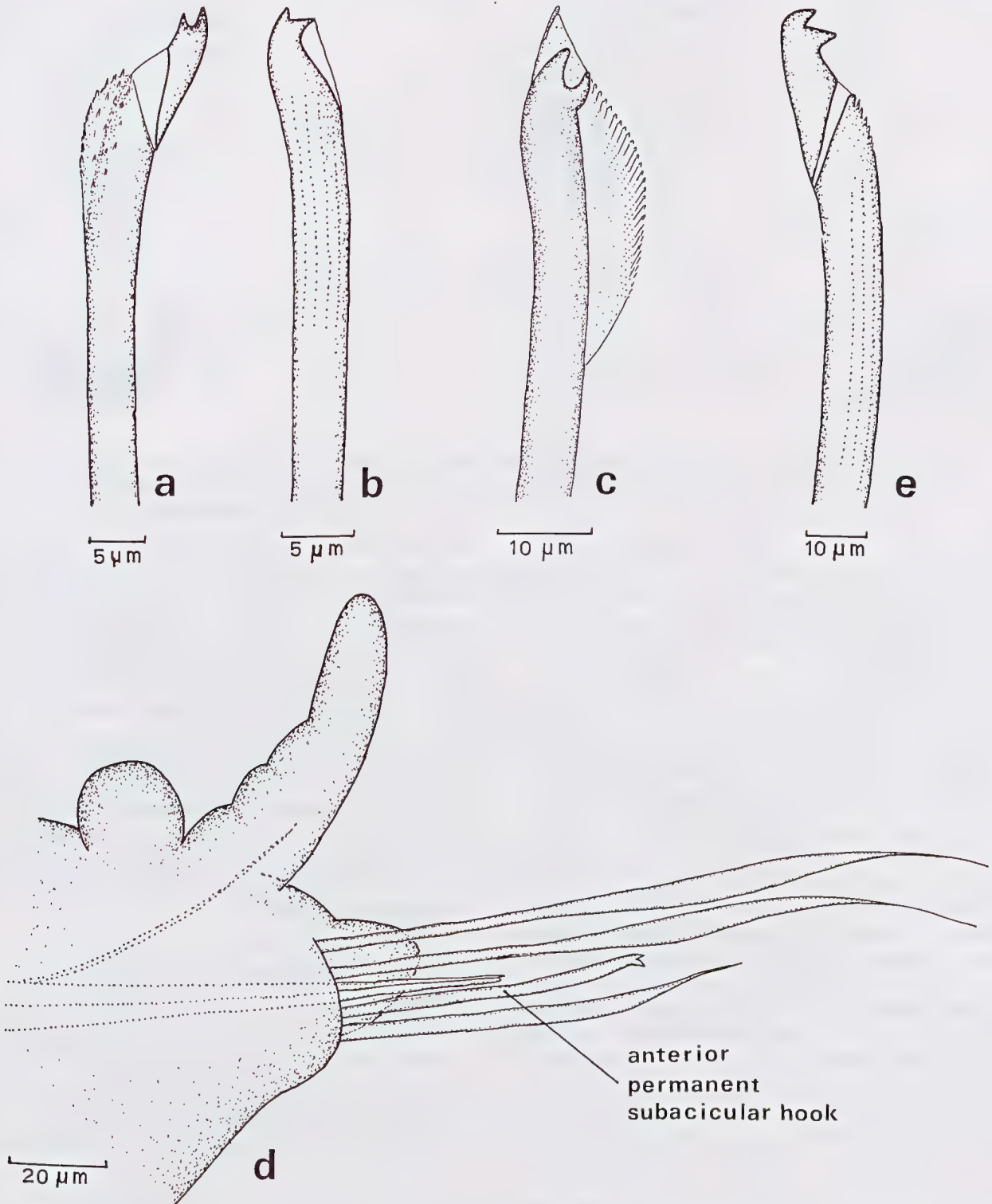


Fig. 13. Larval and juvenile setae: **a**, compound provisional subacicular hook from setiger 7 of 15-setiger embryo of *Onuphis* n. sp.; **b**, anterior permanent subacicular hook from setiger 3 of 65-setiger juvenile of *R. (Rhamphobranchium)* sp.; **c**, simple provisional subacicular hook from setiger 3 of 65-setiger juvenile of *Diopatra* n. sp. 2; **d**, parapodium 6 of 24-setiger juvenile of *Diopatra* n. sp. 2, anterior view; **e**, compound provisional subacicular hook from setiger 49 of 50-setiger juvenile of *Hyalinoecia tubicola*.

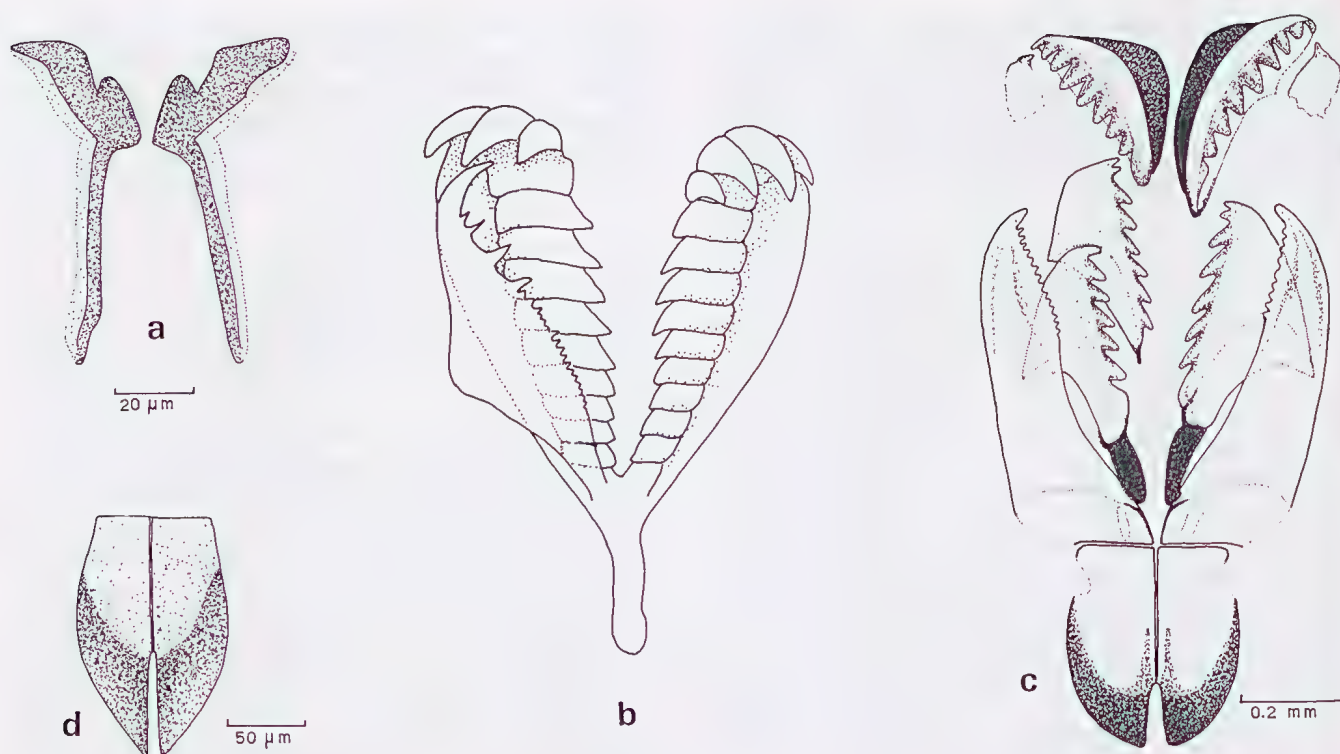


Fig. 14. Larval and juvenile jaws: **a**, mandibles of 40-setiger juvenile of *Diopatra* n. sp. 2; **b**, maxillae of 11-setiger embryo of *Diopatra cuprea* (= *D. sp.*), X680 (from Monro, 1924: fig. 6); **c**, maxillae of 170-setiger juvenile of *Australonuphis* sp. (Mx III to Mx V not in natural position); **d**, carriers of 40-setiger juvenile of *Diopatra* n. sp. 2.

Jaws. The larval mandibles are sclerotized and can be noted as a dark, X-shaped structure (Fig. 14a) through the body wall. This part will be enlarged by the exterior deposition of sclerotized proteins and carbonates, throughout life, at the areas in contact with the cuticular epithelium, i.e. ventrally and laterally. The initial part is still visible in adults dorsally as small dark lines, or in some species it can even be seen in a ventral view through the carbonate layer (Fig. 49g). In decalcified mandibles the initial structures are sometimes longer than the sclerotized plate and have been referred to as 'Stacheln' or thorns by von Haffner (1959).

The development of the larval maxillary apparatus has been described for several species (e.g. *K. elegans*; Blake, 1975) and its function has been observed in live specimens of *Diopatra cuprea* (Allen, 1959). The larval maxillary apparatus (Fig. 14b) can be recognized in a 5-setiger worm and consists of narrow carriers, a pair of maxillae consisting of a series of separate, adjoining pieces, each one with a tooth, and a single left maxilla with small proximal and larger distal teeth. The juvenile apparatus (Fig. 14c) has the typical adult complement of maxillary plates but differs from the adult in detail and proportions. Most of it is very delicate and hardly sclerotized, while the lamellae connecting MxI and Mx II, and the attachment lamellae of Mx IV stand out through their dark sclerotization. Juvenile carriers (Fig. 14c,d) are often posteriorly extended and darkly sclerotized.

Although only on circumstantial evidence, it was assumed that the maxillary apparatuses grow during the

lifetime of the animal (Paxton, 1980) and are not replaced as was previously suggested. Paxton (1980) showed that the number of teeth on Mx II and Mx III increased by the addition of new distal teeth to the plates. Fauchald (1982b) found larval jaw apparatuses in the gut of brooded larvae of *Mooreonuphis jonesi* and interpreted them as shed larval apparatuses. It is likely that the larval jaw apparatus is discarded and replaced by the juvenile one which grows and is retained throughout life. The shedding of the larval maxillae is supported by the lack of observed transition stages between larval and juvenile apparatuses, and the similarity of the larval maxillae to the more ancestral ctenognath maxillae of the family Dorvilleidae which are replaced periodically.

TAXONOMIC ACCOUNT

Evolution within the family Onuphidae has resulted in a radiation of species within a number of evolutionary lines. During the course of this radiation, changes have occurred in the morphology of the various groups as well as their tube consistency and construction, and morphology of oocytes. The taxonomic categories recognized within the family are defined below on the basis of these criteria and consist of two subfamilies and 22 genera (see Table 3 for synopsis).

Table 3. Classification Synopsis of the family Onuphidae

Subfamily	Group	Complex	Genus	Synonym
HYALINOECIINAE new subfam.	Nothria		<i>Nothria</i> Malmgren, 1866	<i>Northia</i> Johnston, 1865
			<i>Anchinotiria</i> n. gen.	—
	Hyalinoecia		<i>Hyalinoecia</i> Malmgren, 1866	<i>Paronuphis</i> Ehlers, 1877
			<i>Leptoecia</i> Chamberlin, 1919	<i>Parhyalinoecia</i> H.-Sch., 1975
ONUPHINAE	Diopatra	Diopatra	<i>Neonuphis</i> Kucheruk, 1978	—
			<i>Hyalospinifera</i> Kuch. 1979b	—
			<i>Notonuphis</i> Kucheruk, 1978	—
		Rhamphobranchium	<i>Paradiopatra</i> Ehlers, 1887	<i>Sarsonuphis</i> Fauch., 1982a
			<i>Diopatra</i> Aud. & M.Edw., 1833	—
			<i>Epidiopatra</i> Augener, 1918	—
	Onuphis	Australonuphis	<i>Brevibrachium</i> n. gen.	—
			<i>Longibrachium</i> n.gen	—
			<i>Rhamphobranchium</i> Ehlers, 1887	<i>Paranorthia</i> Moore, 1903
			<i>Australonuphis</i> Paxton, 1979	<i>Americanuphis</i> Orens., 1974
			<i>Hartmanonuphis</i> n. gen.	—
			<i>Hirsutonuphis</i> n. gen.	—
			<i>Aponuphis</i> Kucheruk, 1978	—
			<i>Kinbergonuphis</i> Fauch., 1982a	—
			<i>Mooreonuphis</i> Fauchald, 1982a	—
			<i>Onuphis</i> Aud. & M. Edw., 1833	—
			<i>Heptaceras</i> Ehlers, 1868	<i>Tradopia</i> Baird, 1870

Key to Genera of Onuphidae

1. Tentacular cirri present (Fig. 3a). 2
- Tentacular cirri absent (Fig. 17a). 16
2. Branchial filaments arranged spirally (Fig. 23d). *Diopatra*
- Branchial filaments arranged otherwise or absent. 3
3. Peristomium middorsally incised (Fig.36a). *Heptaceras*
- Peristomium complete. 4
4. Modified parapodia with extensile setae (shafts extending back through at least 5 segments), usually with spiny shafts and distally recurved. 5
- Modified parapodia with short setae (shafts limited to one segment), usually without spiny shafts, distally uni- to tridentate. 7
5. Three pairs of modified parapodia (with 3 setae each) with spiny shafts and distally recurved (Fig. 27e). *Rhamphobranchium*
- Four to 5 pairs of modified parapodia (with 4 or more setae each) with spiny shafts, or 3 pairs of modified parapodia with smooth shafts. 6
6. Antennae moderately long, to setiger 6-15 (Fig. 26c); 4 pairs of modified parapodia with single postsetal lobes and setae with spiny shafts and distally curved. *Longibrachium*
- Antennae short, to setiger 1; 3-5' pairs of modified parapodia with double postsetal lobes (Fig. 25b) and setae with spiny shafts and distally uni- to tridentate (Fig. 25e,k) or with smooth shafts and distally recurved. *Brevibrachium*
7. Setiger 1 and its parapodia usually enlarged; scoop-shaped pectinate setae (Fig. 15l). 8
- Setiger 1 not enlarged; flat pectinate setae (Fig. 29e). 9
8. Modified parapodia with large, auricular presetal and subulate postsetal lobes (Fig. 15c). *Nothria*

- Modified parapodia with bi- to trilobed presetal and short, subconical postsetal lobes (Fig. 16c). *Anchinothria*
- 9. Tentacular cirri inserted in middle of peristomium (Fig. 28a); modified parapodia directed strongly anteroventrally, ventral cirri of setiger 5 almost touching in ventral midline (Fig. 29a). *Americonuphis*
- Tentacular cirri inserted subdistally to distally on peristomium; modified parapodia directed anteroventrally to -laterally or -dorsally, ventral cirri of setiger 5 far apart. 10
- 10. Pseudocompound hooks of modified parapodia with long, pointed hoods (Fig. 22c,d,j). *Paradiopatra*
- Pseudocompound hooks of modified parapodia with short or without hoods. 11
- 11. Middorsal part of peristomium with anterior fold, separating it from prostomium (Fig. 3a). 12
- Middorsal part of peristomium without anterior fold, appearing to extend to median antenna (Fig. 30a). 14
- 12. Ceratophores of antennae with 10–25 rings, anterior styles shorter than their ceratophores; large median hooks absent. *Onuphis*
- Ceratophores of antennae with 3–7 rings, anterior styles longer than their ceratophores; large median hooks (Fig. 35g) often present. 13
- 13. Compound limbate setae (= spinigers) (Fig. 35h) present in anterior unmodified setigers. *Mooreonuphis*
- Compound limbate setae absent. *Kinbergonuphis*
- 14. Pseudocompound (Fig. 30f) and subacicular hooks (Fig. 30j) distally entire and without hoods. *Australonuphis*
- Pseudocompound hooks uni- to tridentate, subacicular hooks bidentate, both types hooded. 15
- 15. Ceratophores of antennae with 10–15 rings; branchiae from setiger 6–9; maxillary carriers with darkly sclerotized lateral triangles (Fig. 32i). *Hirsutonuphis*
- Ceratophores of antennae with 6–8 rings; branchiae from setiger 1; maxillary carriers without darkly sclerotized lateral triangles (Fig. 31i). *Hartmanonuphis*
- 16. Branchial filaments arranged spirally (Fig. 24d). *Epidiopatra*
- Branchiae absent or as single filaments. 17
- 17. Ceratophores of antennae with 10–20 rings; anterior 5 setigers with hooks. *Aponuphis*
- Ceratophores of antennae with 2–5 rings; anterior 1–3 setigers with hooks. 18
- 18. Modified parapodia with low presetal lobes (Fig. 21d); subacicular hooks in ventral position in fascicle, starting on setiger 9–10. *Notonuphis*
- Modified parapodia with large, auricular presetal lobes (Fig. 17c); subacicular hooks in median position in fascicle (Fig. 17d), starting on setiger 12–35 or later. 19
- 19. Frontal palps well developed; tough, quill-like tubes. *Hyalinoecia*
- Frontal palps reduced or absent; fragile tubes. 20
- 20. Branchiae as single filaments; anterior hooks with pointed hoods (Fig. 20f,g). *Hyalospinifera*
- Branchiae absent; anterior hooks with short, blunt hoods. 21

21. Ceratophores of antennae short ($\frac{1}{3}$ to $\frac{1}{2}$ length of prostomium); tubes flattened with lateral supports. *Leptoecia*
- Ceratophores of antennae very short ($\frac{1}{10}$ length of prostomium); tubes round in transverse section without lateral supports. *Neonuphis*

Family ONUPHIDAE Kinberg

Onuphiacea Kinberg, 1865: 560. Type genus: *Onuphis* Audouin & Milne Edwards, 1833.
Onuphidae Malmgren, 1867: 180.

Diagnosis. Prostomium with 5 dorsal antennae with ceratophores, and 2 frontal palps.

Definition. Prostomium oval to triangular, wider than long; 5 dorsal antennae: pair of anterior lateral, pair of posterior lateral and single median; smooth to ringed ceratophores and distal styles; 2 pairs of ventral palps: smaller frontal palps (rarely absent) and larger posterior bulbous labial palps; eyes present or absent. Nuchal grooves straight to almost circular. Peristomium apodous; pair of dorsal tentacular cirri present or absent; large semilunar lower lip ventrally.

Anterior 1–8 pairs of parapodia modified, with subulate to digitiform ventral cirri, followed by a transition zone of globular ventral cirri, or ventral pads with reduced cirri, thereafter only glandular pads. Dorsal cirri present throughout or reduced to absent on posterior setigers. Branchiae, when present, with simple, pectinately or dichotomously branched, or spirally arranged filaments.

Parapodia subbiramous (with or without reduced notosetae in dorsal cirri). Modified parapodia with simple to pseudocompound hooks, pectinate and/or limbate setae present or absent; setae of unmodified parapodia pectinate, simple to compound limbate (spinigers), rarely falcigers, subacicular hooks. Anal cirri 2 or 4.

Jaws consisting of ventral mandibles and dorsal maxillae formed of $4\frac{1}{2}$ – $5\frac{1}{2}$ pairs of toothed plates and pair of short carriers. Mostly tubicolous. Nurse cells associated with oocytes in 2 strings or cluster.

HYALINOECIINAE n. subf.

Type genus: *Hyalinoecia* Malmgren, 1866.

Diagnosis. Lower limbate setae present to end of body; subacicular hooks in median position in fascicle.

Definition. Frontal palps usually present, rarely absent. Nuchal grooves straight to slightly curved. Peristomium with middorsal anterior fold, ventral lip without median section.

Setiger 1 longer than following setigers. Anterior 1–3 pairs of parapodia modified and directed anteroventrally, parapodia 1 usually prolonged. Presetal lobes of modified parapodia usually auricular, as long as postsetal lobes. Dorsal cirri without basal swelling or process; often reduced to absent in posterior parapodia. Branchiae, when present, with single or dichotomously branched filaments.

Parapodia subbiramous (dorsal cirri without internal notosetae). Hooks of modified parapodia uni- to bidentate. Lower limbate setae simple, present to end of body. Subacicular hooks in median position in fascicle. Two anal cirri.

Mandibles often longer than maxillary carriers and Mx I together. Maxilla III long; Mx VI absent. Nurse cells associated with oocytes attached in single cluster. Tubes circular or oval in transverse section, of translucent substance without external covering; or parchment-like or translucent inner layer, outer layer of foreign particles.

Genus *Nothria* Malmgren

Fig. 15a–n

Nothria Malmgren, 1866: 66. Type species: *Onuphis conchylega* Sars, 1835: 61, by original designation. Gender: feminine.

Northia Johnston, 1865: 136. Preoccupied by *Northia* Gray, 1847 (Mollusca).

Material examined. *Nothria conchylega*—Norway: Ramfjord near Tromsø—5 (AM W.198975) and 2 (AM W.198976). *N. n.sp.*—Australia: Queensland: Fraser Island—4 (AM W.198982).

Diagnosis. Modified parapodia with large, auricular presetal lobes; pectinate setae scoop-shaped.

Definition. Prostomium (Fig. 15a) anteriorly rounded. Posterior antennae on posterior part of prostomium, with smooth ceratophores or with 3–5 rings, and moderately long to long posterior styles: longest (median) to setiger 5–13. Frontal and labial palps oval, latter with small or without median section (Fig. 15b). Nuchal grooves straight with small middorsal separation; peristomium short to moderately long, with distally to subdistally inserted tentacular cirri.

Anterior 2–3 pairs of parapodia modified; parapodia 1 (Fig. 15c) prolonged, with large auricular presetal and subulate postsetal lobes. Anterior dorsal cirri subulate to digitiform, more posterior ones reduced; ventral cirri subulate on anterior 2–3 setigers. Branchiae from setiger 8–13 as single, strap-like filaments, or absent.

Hooks of modified parapodia uni- to bidentate, simple to pseudocompound, with or without blunt hoods (Figs 15d–f,k); scoop-shaped pectinate setae (Fig. 15l) and limbate setae (Fig. 15g,h) from setiger 2; subacicular hooks (Fig. 15i) from setiger 8–14. Pygidium with 2 anal cirri (Fig. 15j).

Jaws with mandibles (Fig. 15m); maxillae (Fig. 15n) with left Mx II with or without distal fang; Mx III distally shorter than left Mx II. Short, flattened tubes, consisting of translucent or parchment-like inner lining and outer layer of foreign particles. Latter consist usually of sand and shell fragments, attached with the flat or concave side to the lining, thus making a flattened

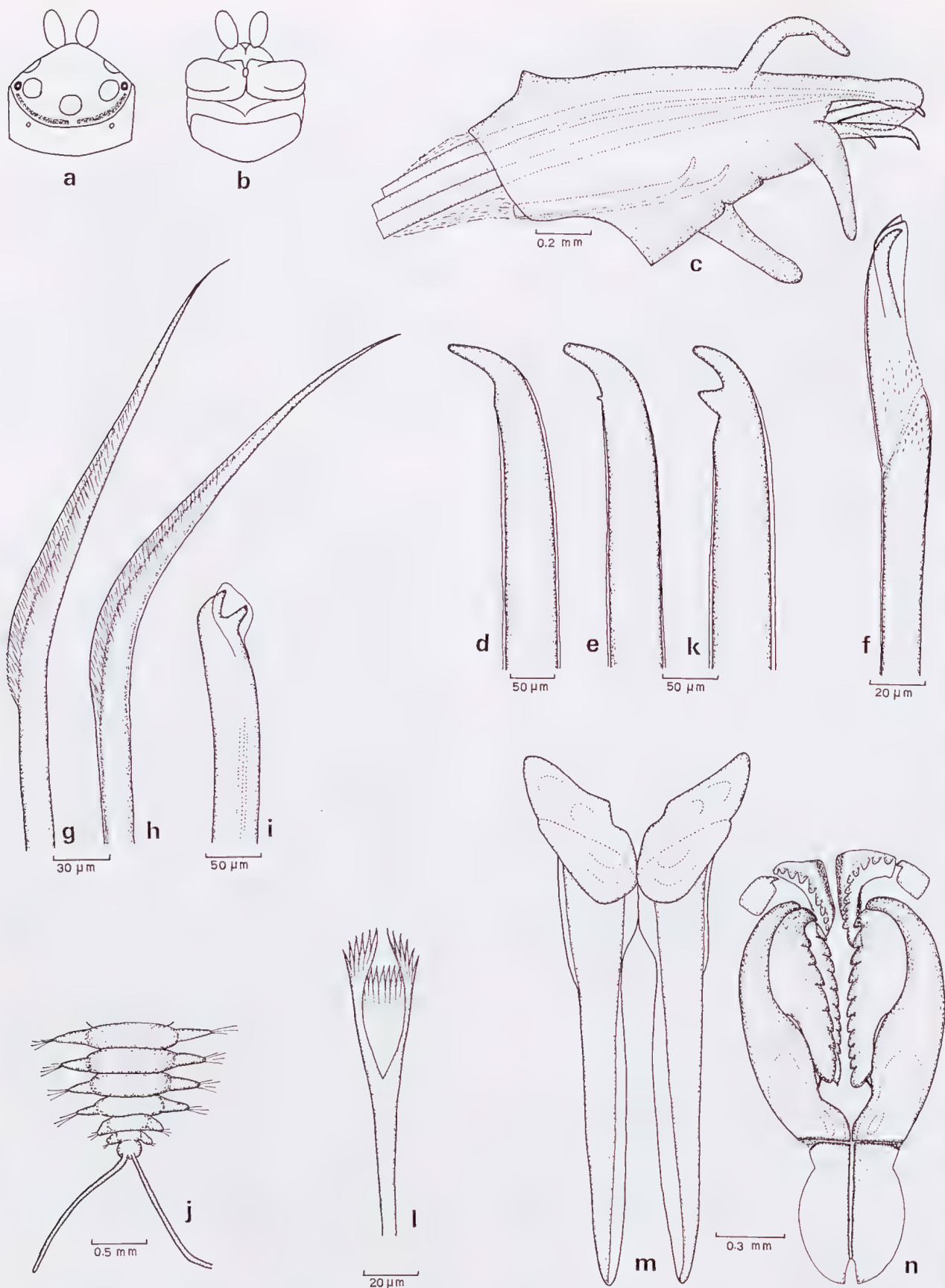


Fig. 15. *Nothria conchylega* (AMS W.198975): **a**, stylized diagram of prostomium and peristomium, dorsal view; **b**, same, ventral view; **c**, parapodium 1, posterior view; **d**, unidentate simple hook from setiger 1; **e**, bidentate simple hook with tiny secondary tooth from same; **f**, unidentate pseudocompound hook from setiger 3; **g**, upper limbate seta from setiger 13; **h**, lower limbate seta from same; **i**, subacicular hook from setiger 30; **j**, posterior end. *Nothria* n. sp. (AMS W.198982): **k**, bidentate simple hook with large secondary tooth from setiger 1; **l**, scoop-shaped pectinate seta from setiger 12; **m**, mandibles; **n**, maxillae.

tube; rod-like lateral supports absent.

Size. Short-bodied with limited number of segments; length to 52 mm for 63 setigers, width to 6 mm with parapodia.

Remarks. Johnston (1865) erected the genus *Northia* for species with single branchial filaments, and included *Nereis tubicola* and *Onuphis conchylega* Sars, 1835. However, *Northia* was preoccupied (*Northia* Gray, 1847 in Mollusca) and was changed to *Nothria* by Malmgren (1866) and the latter species was designated type species. The definition of *Nothria* remained the same and contained species with tentacular cirri, anterior parapodia that were not markedly modified, and branchiae with single filaments or absent. Although it was generally recognized that this was an unnatural grouping and *Nothria* was perhaps a synonym of *Onuphis*, the taxon was retained to separate the large group of species (Hartman, 1944; Fauchald, 1968; 1972; 1977). Some authors treated *Nothria* as a subgenus (Pettibone, 1963; Day, 1967). In 1970 Pettibone redefined *Nothria* on the basis of its type species, *N. conchylega*, and showed that it is characterized by its modified anterior parapodia with specialized setae and flattened tube. This redefinition was followed by Orensanz (1974), Kucheruk (1978), Fauchald (1982a) and is accepted here.

Fauchald (1982a) recognized eight species and gave a key to these. *Nothria abyssia*, *Onuphis africana* and *Paronuphis solenotecton*, referred by Fauchald (1982a) to *Paradiopatra* (= *Anchinothria*), are here considered as species of *Nothria*. Although the types were not examined, the original illustrations show the characteristic auricular presetal lobes. The following species are recognized: *N. conchylega* (Sars, 1835); *N. abyssia* Kucheruk, 1978; *N. africana* (Augener, 1918); *N. anoculata* Orensanz, 1974; *N. atlantica* (Hartman, 1965); *N. australatlantica* Fauchald, 1982c; *N. britannica* (McIntosh, 1903); *N. hawaiiensis* Pettibone, 1970; *N. hyperborea* (Hansen, 1878); *N. mannarensis* Rangarajan & Mahadevan, 1961; *N. occidentalis* Fauchald, 1968; *N. solenotecton* (Chamberlin, 1919); *N. textor* Hartman & Fauchald, 1971; *N. n.sp.*

Distribution. World-wide; shallow to 5200 m.

Anchinothria n. gen.

Fig. 16a-k

Type species: *Diopatra pourtalesii* Ehlers, 1887: 74. Gender: feminine.

Material examined. *Diopatra pourtalesii*—Cuba: near Havana—SYNTYPE (MCZ 687); off Cuba—SYNTYPE (MCZ 815); Caribbean: S of Rebecca Channel—SYNTYPE (tube only) (MCZ 785); Sta. Lucia—2 (ZMH PE-779, PE-782); U.S.A.: Florida—SYNTYPE (MCZ 874). *Paranorthia fissurata*—Mexico: Lower California—HOLOTYPE (USNM 19151). *A. sombreriana*—Caribbean: Sta. Lucia—3 (ZMH PE-782a).

Diagnosis. Modified parapodia with bi- to trilobed presetal lobes; pectinate setae scoop-shaped.

Definition. Prostomium (Fig. 16a) anteriorly rounded. Posterior antennae on posterior part of prostomium, with smooth ceratophores or with 2–5 rings and moderately long to long posterior styles: longest (median) to setiger 5–13. Frontal and labial palps oval, latter with or without distinct distal lobe, without median section (Fig. 16b). Nuchal grooves straight with small middorsal separation; peristomium short to moderately long, with subdistally to distally inserted tentacular cirri.

Anterior 2–3 pairs of parapodia modified; parapodia 1 (Fig. 16c) usually prolonged, with bi- to trilobed presetal and short, subconical postsetal lobes; parapodia 2–3 with shorter presetal and longer, digitiform postsetal lobes. Dorsal cirri subulate to digitiform; ventral cirri subulate on anterior 2–3 setigers. Branchiae from setiger 8–17, as simple strap-like or dichotomously branched filaments (Fig. 16d), or absent.

Hooks of modified parapodia uni- to bidentate, simple to pseudocompound, with or without blunt hoods (Fig. 16e); scoop-shaped pectinate setae (Fig. 16f) and limbate setae (Fig. 16g,h) from setiger 2; subacicular hooks (Fig. 16i) from setiger 8–14.

Jaws with mandibles (Fig. 16j), and maxillae (Fig. 16k) with left Mx II with distal fang, Mx III distally shorter than left Mx II. Short to moderately long, round or flattened tubes, consisting of translucent or parchment-like inner lining, with or without thin outer layer of mud, and with scattered foreign materials. Latter consisting often of rod-like pieces, e.g. glass sponge spicules, echinoid spines, even pine-needles, often used as lateral supports.

Size. Short-bodied with limited number of segments (complete specimen of *A. cirrobranchiata* measures 35 mm long for 55 setigers, 3 mm wide) to moderately long (up to 112 mm for 100 setigers, width 7 mm).

Etymology. The name *Anchinothria* is derived from the Greek *anchi* for near and *Nothria*, emphasizing the close relationship between the two genera.

Remarks. The genus *Anchinothria* is erected for those species that were referred by Pettibone (1970) and Fauchald (1982a) to *Paradiopatra* Ehlers. As discussed below (see 'Remarks' for *Paradiopatra*) the first designated type species of *Paradiopatra*, *Diopatra* (*Paradiopatra*) *fragosa* Ehlers, 1887, is not congeneric with the species of *Paradiopatra* as defined by Pettibone (1970) and Fauchald (1982a).

The type species of *Anchinothria*, *Diopatra pourtalesii*, can be recognized by its characteristic tubes, which are flattened, have laterally attached supports consisting of echinoid spines or skeletal parts of other animals and are sometimes covered with transversely attached glass sponge spicules. This type of tube was first mentioned by Pourtales (1869), and the tube only was described by Ehlers (1879) as *Diopatra pourtalesii* in a preliminary report. Ehlers (1887) gave a complete description of the animal and listed seven localities in the Caribbean for his specimens, most of which are in the collections of the MCZ. These syntypes were

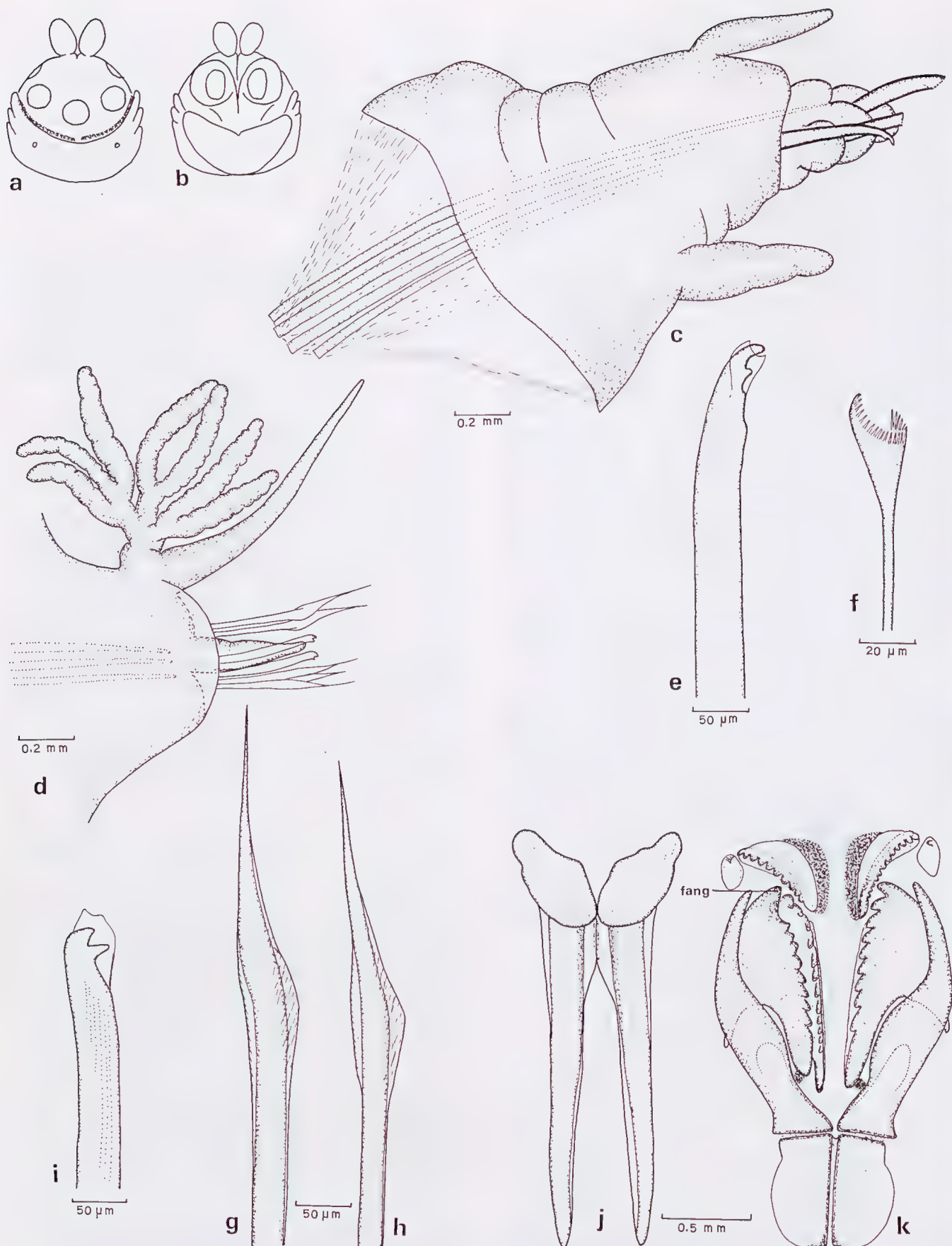


Fig. 16. *Anchinothria pourtalesii* (ZMH PE-779): **a**, stylized diagram of prostomium and peristomium, dorsal view; **b**, same, ventral view; **c**, parapodium 1, anterior view; **d**, parapodium 14, anterior view; **e**, bidentate pseudocompound hook from setiger 1; **f**, scoop-shaped pectinate seta from setiger 14; **g**, upper limbate seta from same; **h**, lower limbate seta from same; **i**, subacicular hook from same; **j**, mandibles; **k**, maxillae.

examined by Fauchald (1982a) who stated that none were specifically mentioned by Ehlers (1887). Two specimens, not listed among the original localities, with the following label: 'Diopatra Pourtalesi Ehl., Depth 422 fms., Sta. Lucia, A. Agassiz 1878/79', were apparently retained by Ehlers and are now in the collections of the ZMH. The branchiae commence at setiger 9–10 in one specimen (PE-779) and 11 in the other (PE-782), and have a maximum of 7–9 filaments. The syntypes at the MCZ have branchiae from setiger 9–12, and maximally 4–5 filaments. In the description, Ehlers stated that branchiae originate on setigers 7–9, and have maximally 8 filaments, while in the figured specimen (pl. 19 fig. 6), they start at setiger 10. It is more likely that the description is based on the specimens retained in Germany (and Fig. 6 on specimen PE-782) than those deposited at the MCZ.

The anterior pseudocompound hooks are bidentate (Fig. 16e) but they are unusual in that the hood originates far distally from a protrusion that could be interpreted as a third tooth, as was done by Fauchald (1982a). The branchiae (Fig. 16d) appear in a bundle with each initial branch usually giving rise to two, rarely three filaments. This arrangement has been clearly illustrated by Ehlers (1887: pl. 19 fig. 10) and Pettibone (1970: figs 61h,k). Fauchald (1982a) described the branching as 'clearly pectinate'. The syntypes were examined in the present study and found to have dichotomously branched branchiae as well. However, since they have only 4–5 branchial filaments, the true pattern is not as obvious as in the larger specimens.

The following species are referred to *Anchinotheria*. This list is, with some modifications, based on Fauchald (1982a) who gave a key to species (= *Paradiopatra*): *Diopatra pourtalesii* Ehlers, 1879; *Nothria abbranchiata* McIntosh, 1885; *Paranorthia antarctica* Hartman, 1967b; *Onuphis cirrobranchiata* Moore, 1903; *Onuphis cobra* Chamberlin, 1919; *Onuphis crassisetosa* Chamberlin, 1919; *Paranorthia fissurata* Fauchald, 1972; *Diopatra (Paradiopatra) glutinatrix* Ehlers, 1887; *Nothria hiatidentata* Moore, 1911; *Nothria macrobranchiata* McIntosh, 1885; *Nothria pycnbranchiata* McIntosh, 1885; *Nothria sombreroana* McIntosh, 1885.

Distribution. World-wide; in 36–3931 m, most species deeper than 500 m (see Fauchald, 1982a).

Genus *Hyalinoecia* Malmgren

Fig. 17a–l

Hyalinoecia Malmgren, 1866: 67. Type species: *Nereis tubicola* Müller, 1776: 18, by monotypy. Gender: feminine.

Paronuphis Ehlers, 1887: 78. Type species: *Onuphis (Paronuphis) gracilis* Ehlers, 1887: 78, by monotypy.

Material examined. *Hyalinoecia tubicola*—Australia: Tasmania—4 (AM W.198988) and 2 (NMV). *H. nr tubicola*—Australia: Western Australia—6 (WAM 57-79) and others (WAM). *Paronuphis bermudensis*—Bermuda: HOLOTYPE (AHF Poly 0734); Brazil: Pernambuco—5 (AHF). *H. ?brevicornis*—Australia: Queensland: Fraser Island—9 (AM W.198987). *H. sp.*—Australia: New South Wales: off

Wollongong—4 (AM W.198989).

Diagnosis. Frontal palps well developed; subacicular hooks in median position; maxilla V present; tubes secreted entirely by inhabitants, round in transverse section, without lateral supports.

Definition. Prostomium (Fig. 17a) anteriorly rounded. Posterior antennae on posterior part of prostomium, with ceratophores with 2–5 rings and long styles: longest (median) to setiger 8–14. Frontal palps rounded to subulate; labial palps rounded, without median section (Fig. 17b). Nuchal grooves straight with small to moderately large middorsal separation; peristomium short to moderately long; tentacular cirri absent.

Anterior 2–3 pairs of parapodia (Fig. 17c) modified; parapodia 1 (often also 2 and 3) prolonged, with large auricular presetal and subulate postsetal lobes. Anterior dorsal cirri large, later ones reduced; ventral cirri digitiform on anterior 3–4 setigers. Branchiae from setiger 18–33, as single, strap-like filaments (Fig. 17d), or absent.

Hooks of modified parapodia uni- to bidentate, simple to pseudocompound, with or without hoods (Fig. 17e,f); flat pectinate setae (Fig. 17g) and limbate (Fig. 17h,i) setae from setiger 2; subacicular hooks (Fig. 17j) from setiger 15–30.

Jaws with mandibles (Fig. 17k) and maxillae (Fig. 17l). Tubes longer than inhabitants, round in transverse section, quill-like, with internal valves; of translucent, usually tough substance, without external covering of foreign particles.

Size. Small to moderately large; length to 18 cm, width to 6 mm.

Remarks. Blainville (1828) provided the name *Nereitube* as a genus for *Nereis tubicola* Müller. However, this name is vernacular and thus considered as invalid.

Paronuphis Ehlers, 1887 was characterized as an abbranchiate, *Hyalinoecia*-like genus. Augener (1906) pointed out that the type species, *O.(P.) gracilis*, represented a juvenile *Hyalinoecia* and referred it to this genus, a decision which has more recently been supported by Mangum & Rhodes (1970) who believed that *O.(P.) gracilis* is an intermediate between juvenile and adult forms of *H. artifex*.

Hartman (1965) described the abbranchiate *Paronuphis bermudensis* and distinguished it from *O.(P.) gracilis* by having long-appendaged, composite falcigers in the anterior parapodia, and very short-appendaged, composite falcigers (= compound subacicular hooks) in posterior segments. These typical juvenile characters are present in the holotype while larger specimens from station Ch35Dr12 have simple to short-appendaged pseudocompound hooks in setigers 1 and 2, but still have compound posterior subacicular hooks and are still abbranchiate. Hartman mentioned a specimen from sta. Be7 with ova and embryos in its body cavity, demonstrating the maturity of these small specimens. Unfortunately, this particular specimen cannot be

located [Williams (AHF), personal communication].

Small abbranchiate species are found in several onuphid genera in which most species have branchiae. This condition is not considered to be of generic status. Hence, in agreement with Kucheruk (1978), *Hyalinoecia* is here defined as having single branchial filaments or being abbranchiate, and *Paronuphis bermudensis* Hartman, 1965 is referred to *Hyalinoecia*.

Fauchald (1977) recognized 20 species.

Distribution. World-wide; shallow to 2448 m.

Genus *Leptoecia* Chamberlin

Fig. 18a-h

Leptoecia Chamberlin, 1919: 319. Type species: *Leptoecia abyssorum* Chamberlin, 1919: 320, by original designation.

Gender: feminine.

Parhyalinoecia Hartmann-Schröder, 1975: 65. Type species:

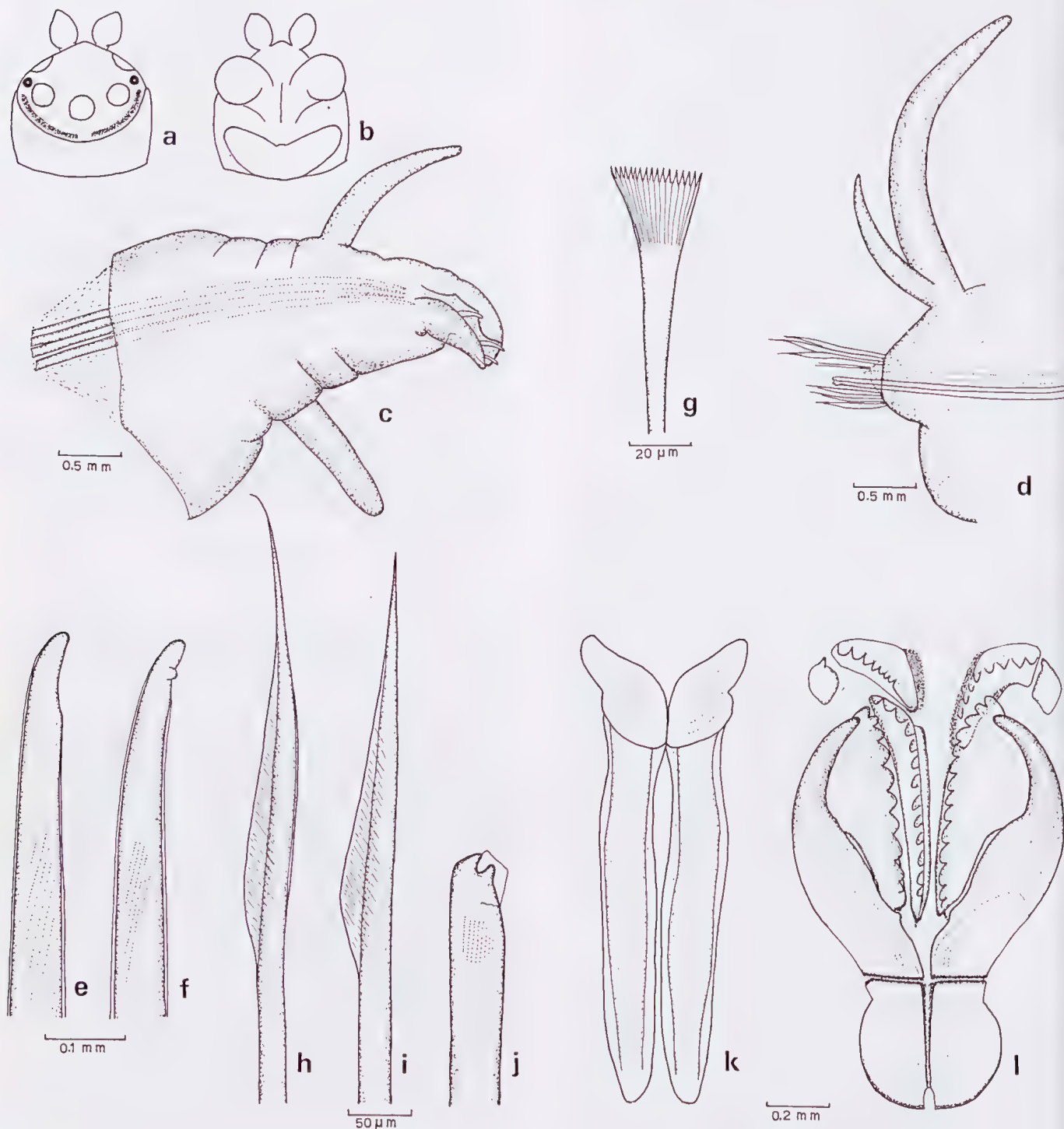


Fig. 17. *Hyalinoecia tubicola* (AM W.198988): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, parapodium 1, posterior view; d, parapodium 29, anterior view; e, unidentate simple hook from setiger 1; f, bidentate simple hook from same; g, pectinate seta from setiger 29; h, upper limbate seta from same; i, lower limbate seta from same; j, subacicular hook from same; k, mandibles; l, maxillae.

Parhyalinoecia apalpata Hartmann-Schröder, 1975: 65, by original designation.

Material examined. *Leptoecia abyssorum*—Ecuador—HOLOTYPE (USNM 19406). *Parhyalinoecia apalpata*—Portugal—HOLOTYPE (ZMH P-13630).

Diagnosis. Frontal palps reduced or absent; tubes secreted entirely by inhabitants, oval in transverse section, with lateral thickenings on both sides.

Definition. Prostomium (Fig. 18a) anteriorly rounded. Posterior antennae on posterior part of prostomium with short ceratophores ($\frac{1}{3}$ – $\frac{1}{2}$ length of prostomium), smooth or with 2–4 indistinct rings, and long styles. Frontal palps reduced to ventral semicircular protrusions, or absent; labial palps reduced (Fig. 18b). Nuchal grooves slightly curved; peristomium short to

long with weakly defined ventral lip; tentacular cirri absent.

Anterior 1–2 pairs of parapodia modified. Parapodia 1 (Fig. 18d) prolonged, with auricular presetal and subulate postsetal lobes; parapodia 2 shorter, presetal lobes low, postsetal lobes subconical to digitiform. Dorsal cirri subulate on anterior setigers, reduced in median and absent in posterior region; ventral cirri subulate on anterior 2 setigers. Branchiae absent.

Hooks of modified parapodia uni- to bidentate, simple with hoods (Fig. 18c,e); flat pectinate setae and limbate setae (Fig. 18f) from setiger 2; subacicular hooks (Fig. 18g) from setiger 35 or later.

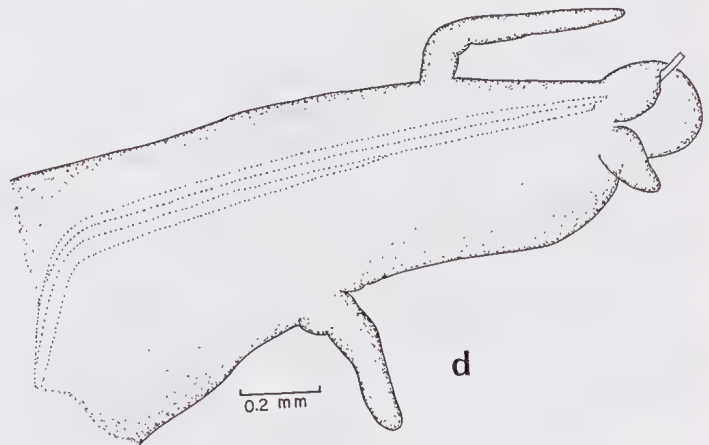
Mandibles with large initial parts; Mx I to Mx III with large cavity openings (Fig. 18h), left Mx II with distal fang, long Mx III, Mx V absent. Tubes thin, translucent,



a



b



d

20 μ m

f

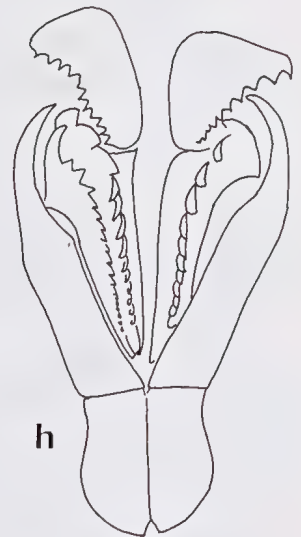
g



e



c



h

Fig. 18. *Leptoecia apalpata* (a, b, holotype ZMH P-13630; c, from Hartmann-Schröder, 1975: fig. 36): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, bidentate simple hook from setiger 1. *Leptoecia abyssorum* (d, f, g, holotype USNM 19406); e, h, from Chamberlin, 1919: figs 8, 3): d, parapodium 1, posterior view; e, unidentate simple hook from setiger 1; f, spiny limbate seta from setiger 2; g, subacicular hook from setiger 49; h, maxillae.

longer than inhabitants; oval in transverse section, with thickenings on both sides; without external covering of foreign particles.

Size. Small; to 42 mm for 70 setigers, width 1.75 mm.

Remarks. *Leptoecia* was considered as a junior synonym of *Paronuphis* Ehlers, 1887 (Hartman, 1965; Fauchald, 1977). However, *Paronuphis* is an invalid genus (see 'Remarks' for *Hyalinoecia*). Kucheruk (1978) resurrected *Leptoecia*, emphasizing not only morphological characters but also the method of tube construction in the definition of the genus.

Hartmann-Schröder (1975) described the monotypic genus *Parhyalinoecia*, characterized by the absence of frontal and labial palps. The holotype of *P. apalpata* was examined and found to lack frontal palps but weakly defined labial palps are present. The ceratophores of the antennae are longer than shown by Hartmann-Schröder (1975: fig. 32). *Parhyalinoecia apalpata* is insufficiently different from *L. abyssorum* to warrant separate generic status. Both species construct the characteristic tubes, distinct from those known for any other onuphids. Kucheruk (1978) erroneously stated that *P. apalpata* constructs round tubes. *Parhyalinoecia* is here considered a junior synonym of *Leptoecia*.

The following species are recognized: *L. abyssorum* Chamberlin, 1919; *L. apalpata* (Hartmann-Schröder, 1975).

Distribution. Pacific Ocean: Mexico, Galapagos Islands, Ecuador, Coral Sea, Tasmania; Indian Ocean: Arabian Sea; North Atlantic Ocean: Portugal; in 2880–5275 m.

Key to Species of *Leptoecia*

- Peristomium as long as setiger 1; unidentate hooks (Fig. 18d) on setiger 1 only. *L. abyssorum*
- Peristomium half as long as setiger 1; bidentate hooks (Fig. 18c) on setigers 1 and 2. *L. apalpata*

Genus *Neonuphis* Kucheruk

Fig. 19a–h

Neonuphis Kucheruk, 1978: 93. Type species: *Neonuphis oxyrhinchus* Kucheruk, 1978: 93, by original designation. Gender: feminine.

Material examined. *Hyalinoecia benthaliana*—New Zealand: SE of North Island—LECTOTYPE (BMNH ZK 1885.12.1.233). *Neonuphis benthaliana*—Antarctica: South Shetland Islands—2 (USNM 58396); Antarctic Peninsula—2 (USNM 58399); Mid-Pacific Antarctic Basin—2 (USNM 58405).

Diagnosis. Frontal palps reduced or absent; maxilla V absent; tubes secreted entirely by inhabitants, round in transverse section, without lateral thickenings.

Definition. Prostomium (Fig. 19a) anteriorly rounded

or pointed. Posterior antennae on posterior part of prostomium, with very short, smooth ceratophores ($\frac{1}{10}$ length of prostomium), and short to moderately long styles: longest (median) to setiger 2–8. Frontal palps reduced to ventral semicircular protrusions or absent; labial palps reduced (Fig. 19b). Nuchal grooves slightly curved, with moderate middorsal separation; peristomium short; tentacular cirri absent.

Anterior 1–2 pairs of parapodia modified. Parapodia 1 (Fig. 19c) prolonged, with auricular presetal and subulate postsetal lobes (latter may be absent in *N. oxyrhinchus*); parapodia 2 shorter, presetal lobes low, postsetal lobes longer, digitiform. Dorsal cirri subulate on anterior setigers, reduced or absent from setiger 7–14; ventral cirri subulate on anterior 2 setigers. Branchiae absent.

Hooks of modified parapodia bidentate, simple to pseudocompound with hoods (Fig. 19d); flat pectinate setae and limbate setae (Fig. 19e) from setiger 2; subacicular hooks (Fig. 19f) from setiger 12–30.

Mandibles (Fig. 19g) with large initial parts; Mx I to Mx III with large cavity openings (Fig. 19h), left Mx II with or without distal fang, long Mx III, Mx V absent. Tubes translucent; longer than inhabitants; round in transverse section, without external covering of foreign particles.

Size. Small; length to 42 mm for 75 setigers, width to 1.5 mm.

Remarks. *Neonuphis* was described by Kucheruk as a monotypic genus for *N. oxyrhinchus*, and defined as lacking frontal and labial palps, possessing one pair of prolonged anterior parapodia with large rounded postsetal lobes, bidentate compound hooks, and constructing *Hyalinoecia*-like, round, translucent tubes. Unfortunately, the specimens were not available for examination. Auricular presetal lobes are present in all genera of the Hyalinoeciini. The lobes designated as 'postsetal' by Kucheruk appear as typical presetal lobes in his figures and are here considered as such. The 'real' postsetal lobes, usually of subulate shape, may have been lost; it is unlikely that they are absent in *N. oxyrhinchus*.

Neonuphis, as presently defined, is very close to *Leptoecia*. The distinguishing characters are the longer ceratophores in *Leptoecia*, and different tube construction. As more material becomes available, *Neonuphis* may prove to be a junior synonym of *Leptoecia*.

Kucheruk (1978) erroneously stated that *Parhyalinoecia apalpata* Hartmann-Schröder, 1975 construct similar tubes to *Neonuphis*. He distinguished *Parhyalinoecia* from *Neonuphis* by the presence of spiky limbate setae and dorsal cirri on all segments in the former, and smooth limbate setae and absence of dorsal cirri after setiger 7–8 in the latter. Kucheruk (1978) referred *Hyalinoecia benthaliana* McIntosh, 1885 and *Paronuphis ultraabyssalis* Kucheruk, 1977 to *Parhyalinoecia*. *Parhyalinoecia* was found to be a junior synonym of *Leptoecia* (see 'Remarks' for *Leptoecia*);

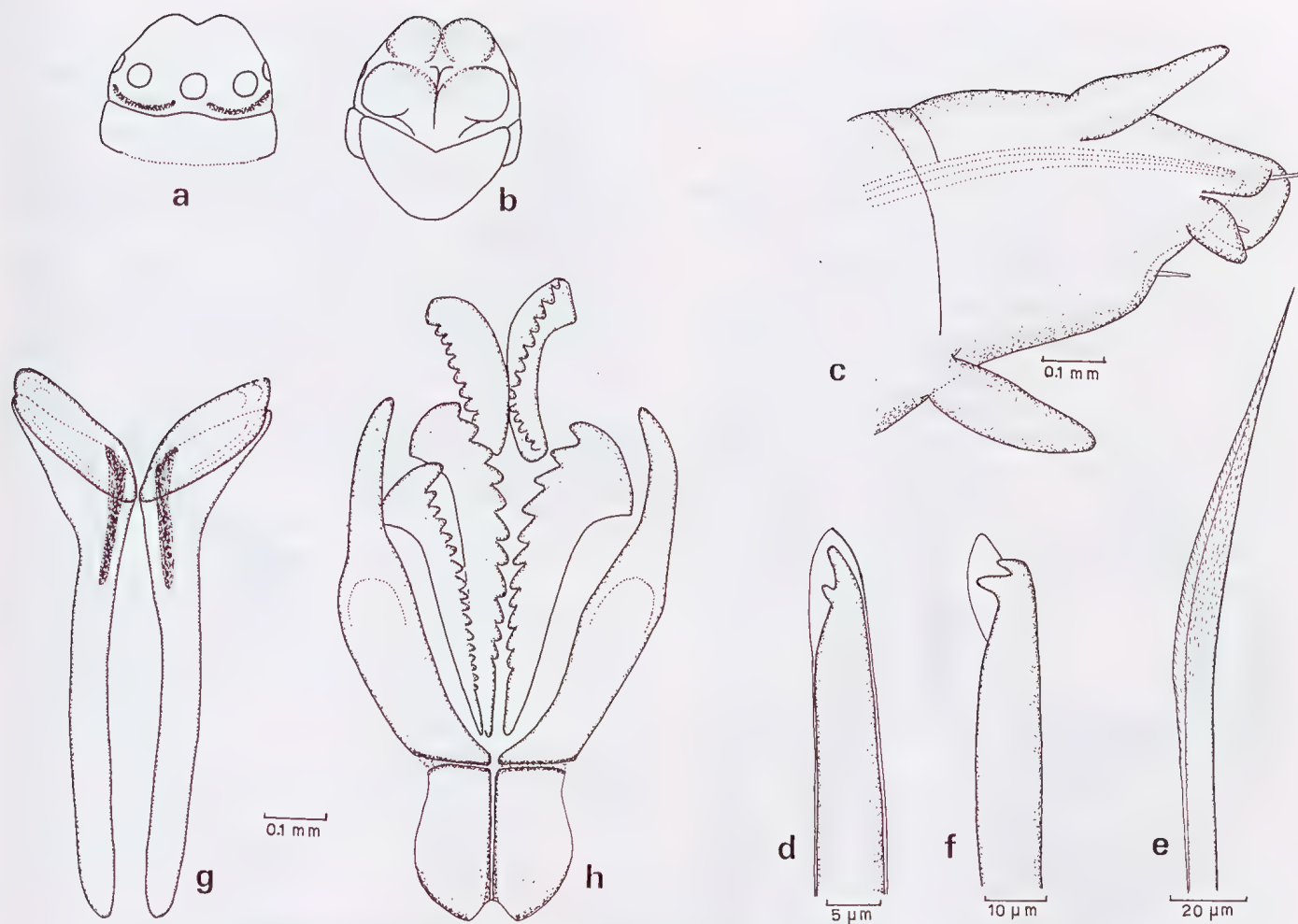


Fig. 19. *Neonuphis benthaliana* (a–c, g–h USNM 58405; d–f, lectotype BMNH ZK 1885.12.1.233): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, parapodium 1, posterior view; d, bidentate simple hook from setiger 1; e, limbate seta from setiger 8; f, subacicular hook from median setiger; g, mandibles; h, maxillae.

it constructs tubes which are flattened and are supported by two lateral thickenings. Spiky limbate setae are not considered a distinctive generic character as they occur in species of other genera (e.g. *Rhamphobranchium diversosetosum*). Dorsal cirri are reduced or absent after the anterior setigers in most Hyalinoeciinae, as indeed they are also in *Parhyalinoecia apalpata*.

Hyalinoecia benthaliana and *Paronuphis ultraabyssalis* are herewith referred to *Neonuphis*.

The two syntypes of *H. benthaliana* were examined; both specimens are in poor conditions. One syntype (BM ZK 1885.12.1.233) is in three pieces; part of the prostomium and the jaw apparatus is missing. Part of the tube is preserved and consists of translucent fragments without lateral thickenings. This is the specimen from station 168 upon which McIntosh based most of the description, and it is herewith designated the lectotype. The other syntype (BM ZK 1885.12.1.234) is the dried specimen from station 158. It consists of part of the prostomium and 10 segments, although an unknown number of anterior segments is missing. With the specimen is part of a tube, consisting of a yellowish, translucent substance with a thickening on one side as characteristic of *Hyalospinifera*. McIntosh stated that the specimen had simple branchiae, a character that is

also present in *Hyalospinifera*, but absent in the lectotype of *Hyalinoecia benthaliana*. However, most setae are broken and the anterior parapodia which carry the characteristic hooks with pointed hoods in *Hyalospinifera spinosa* are lost. No definitive identification can be made and the specimen is herewith designated as *Hyalospinifera* sp.

Some of the specimens reported by Hartman (1967b) as *Paronuphis benthaliana* were examined and found to agree with the original description and the remains of the lectotype.

The following species are recognized: *N. oxyrhinchus* Kucheruk, 1978; *N. benthaliana* (McIntosh, 1885); *N. ultraabyssalis* (Kucheruk, 1977).

Distribution. Pacific Ocean: Philippino Trough, New Zealand, South of Australia, Antarctic; Atlantic Ocean: Antarctic; in 720–6330 m.

Key to Species of *Neonuphis*

1. Prostomium anteriorly pointed; dorsal cirri absent after setiger 7–8. . . . *N. oxyrhinchus*
- Prostomium anteriorly rounded (Fig. 19a); dorsal cirri distinct to setiger 14 or later. 2

2. Bidentate hooks of setiger 1 simple (Fig. 19d); subacicular hooks from setiger 22–29. *N. benthaliana*

—Bidentate hooks of setiger 1 pseudocompound; subacicular hooks from setiger 12–13. *N. ultraabyssalis*

Genus *Hyalospinifera* Kucheruk

Fig. 20a–n

Hyalospinifera Kucheruk, 1979b: 1585. Type species:

Hyalospinifera spinosa Kucheruk, 1979b: 1585, by original designation. Gender: feminine.

Material examined. *Hyalinoecia benthaliana*—Australia: S of Australia—SYNTYPE (BMNH ZK 1885.12.1.234).

Diagnosis. Frontal palps reduced; anterior hooks with pointed hoods; tubes secreted entirely by inhabitants, egg-shaped in transverse section, with lateral thickenings on one side.

Definition. Prostomium (Fig. 20a) anteriorly rounded. Posterior antennae on median part of prostomium, with short ceratophores with 3–4 indistinct

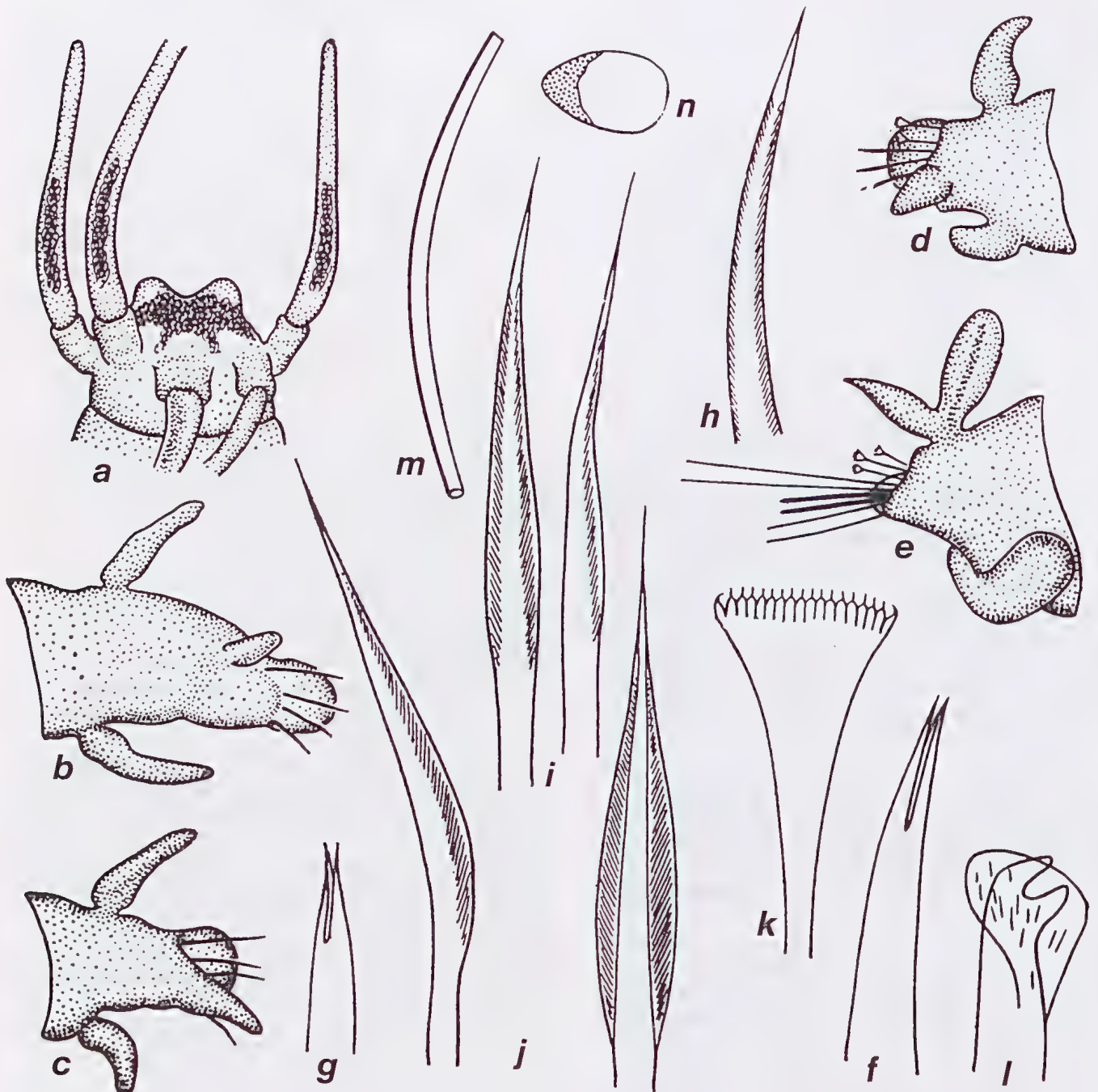


Fig. 20. *Hyalospinifera spinosa* (from Kucheruk, 1979: figs 1–14): a, prostomium, dorsal view; b, parapodium 1, posterior view; c, parapodium 2, same view; d, parapodium 3, same view; e, parapodium 25, anterior view; f, simple hook with pointed hoods from setiger 1; g, same from setiger 2; h, limbate seta from setiger 1; i, same from setiger 3; j, same from setiger 18; k, pectinate seta from setiger 3; l, subacicular hook from setiger 25; m, tube; n, transverse section of tube.

rings, and long styles. Frontal palps semicircular, labial palps rounded. Nuchal groove presumably straight; tentacular cirri absent.

Anterior 2 pairs of parapodia modified. Parapodia 1 (Fig. 20b) prolonged, with auricular presetal and short, digitiform postsetal lobes; parapodia 2 and 3 (Fig. 20c,d) shorter, presetal lobes shorter, postsetal lobes longer, subconical. Dorsal cirri subulate to digitiform, ventral cirri digitiform on 2–3 setigers. Branchiae (Fig. 20e) from setiger 16–18, simple filaments throughout.

Hooks of modified parapodia with pointed hoods (Fig. 20f,g) on setigers 1–2; limbate setae (Fig. 20h–j) from setiger 2; flat pectinate setae (Fig. 20k) from setiger 3; subacicular hooks (Fig. 20l) from setiger 18–19.

Details of jaw apparatus not known. Tubes (Fig. 20m) bent, translucent; egg-shaped in transverse section (Fig. 20n) with thickening on one side; without external covering of foreign particles.

Size. Small; length of incomplete holotype 20 mm for 42 setigers, width 1.3 mm.

Remarks. No specimens were available for examination. One syntype of *Hyalinoecia benthaliana* (BM ZK 1885.12.1.234) is considered as an unidentifiable species of *Hyalospinifera* (see 'Remarks' for *Neonuphis*).

Distribution. Southern Indopacific: Arabian Sea, Bay of Bengal, Indonesia, South of Australia; in 850–3294 m.

Subfamily ONUPHINAE

Type genus: *Onuphis* Audouin & Milne Edwards, 1833.

Diagnosis. Lower limbate setae absent posterior to origin of subacicular hooks; subacicular hooks in median position in fascicle.

Definition. Frontal palps present. Nuchal grooves straight to almost circular. Peristomium with or without middorsal anterior fold, ventral lip with median section.

Setiger 1 usually same length as following setigers. Anterior 2–8 pairs of parapodia modified. Presetal lobes of modified parapodia usually short, half as long as postsetal lobes. Dorsal cirri present on all setigers; often with basal swelling, rarely with basal process. Branchiae, when present, with simple, pectinately branched or spirally arranged filaments.

Parapodia subbiramous, dorsal cirri usually with internal notosetae (absent only in *Notonuphis*). Hooks of modified parapodia uni- to tridentate. Lower limbate setae usually simple, rarely pseudocompound or compound (= spinigers), absent posterior to origin of subacicular hooks; latter in ventral position in fascicle. Four anal cirri.

Mandibles as long as maxillary carriers and Mx I together. Maxilla III short to long, Mx VI rarely present. Nurse cells associated with oocytes attached in 2 strings. Tubes circular in transverse section, parchment-like or mucous inner layer, outer layer of foreign particles usually present.

Genus *Notonuphis* Kucheruk

Fig. 21a–i

Notonuphis Kucheruk, 1978: 93. Type species: *Leptoecia antarctica* Monro, 1930: 133, by original designation. Gender: feminine.

Material examined. *Notonuphis antarctica*—Antarctica: Bransfield Strait—many (USNM 58411). *Nothria minuta*—New Zealand—HOLOTYPE (BMNH ZK 1885.12.1.227).

Diagnosis. Frontal palps globular; tentacular cirri absent; branchiae absent; setiger 1 not prolonged.

Definition. Prostomium (Fig. 21a) short, anteriorly rounded. Posterior antennae on posterior part of prostomium, with ceratophores with 3–4 rings, with moderately long styles: longest styles (posterior laterals) to setiger 5–9. Frontal and labial palps rounded, latter without distal lobes or median section (Fig. 21b). Nuchal grooves straight, peristomium moderately long, with middorsal anterior fold, ventral lip with small median section. Tentacular cirri absent.

Anterior 3 pairs of parapodia modified, not prolonged (Fig. 21c,d). Dorsal cirri without internal setae; ventral cirri subulate on anterior 2–3 setigers, short transition zone of globular ventral cirri. Branchiae absent.

Hooks of modified parapodia pseudocompound to simple, uni- to bidentate with long hoods (Fig. 21e). Pectinate setae (Fig. 21f) from setiger 10, upper limbate setae from setiger 1, lower limbate setae simple; bidentate hooded subacicular hooks (Fig. 21g) from setiger 9–10.

Jaws with mandibles, and maxillae (Fig. 21h) with long Mx III, Mx V moderately large, Mx VI absent. Tubes consisting of tough inner parchment-like layer and outer layer of mud.

Size. Small; length to 65 mm (115 setigers), width to 1.5 mm.

Remarks. *Nothria minuta* McIntosh, 1885 was considered an indeterminable species of *Hyalinoecia* by Fauchald, 1982a. The holotype, which is lacking its prostomium and immediate anterior setigers, was examined in the present study. The median setigers (Fig. 21i) lack branchiae and dorsal setae, have oblique pectinate setae, and subacicular hooks with very short upper teeth. The original description and illustrations showed that the animal lacked tentacular cirri and possessed simple, curved bidentate hooks with long pointed hoods on setiger 1, and the maxillary apparatus had a long Mx III. The combination of these characters marks *Nothria minuta* a member of *Notonuphis*, to which it is referred herewith as the second known species of the genus.

Distribution. Southern oceans: Antarctic and New Zealand; 175–1437 m.

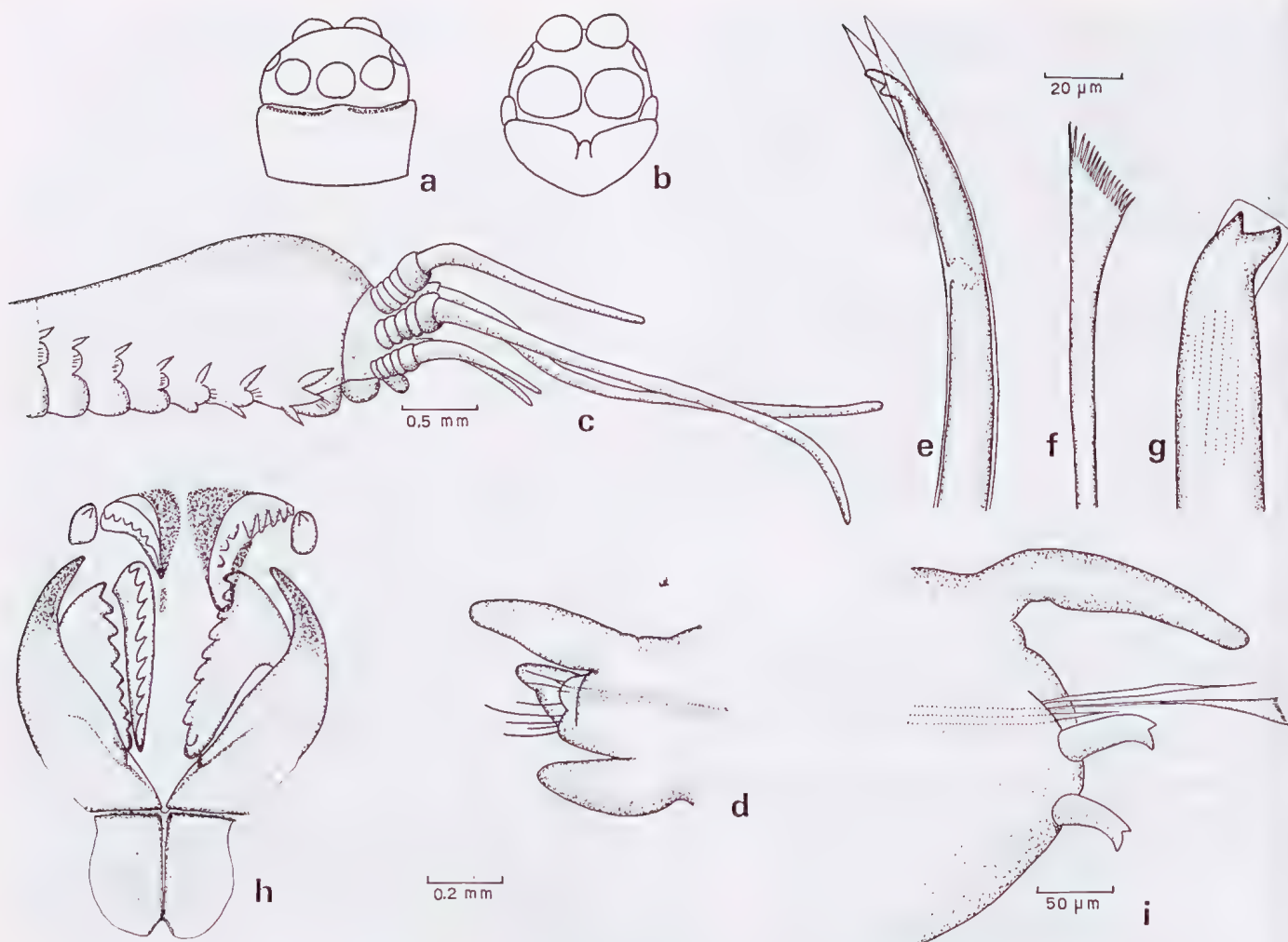


Fig. 21. *Notonuphis antarctica* (USNM 58411): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, anterior end, lateral view; d, parapodium 1, anterior view; e, pseudocompound hook from setiger 1; f, pectinate seta from setiger 30; g, subacicular hook from same; h, maxillae. *N. minuta* (holotype BMNH ZK 1885.12.1.227): i, median setiger.

Key to Species of *Notonuphis*

- Pseudocompound hooks on setiger 1 (Fig. 21e). *N. antarctica*
- Simple hooks on setiger 1. *N. minuta*

Genus *Paradiopatra* Ehlers

Fig. 22a–k

Diopatra (*Paradiopatra*) Ehlers, 1887: 73. Type species: *Diopatra* (*Paradiopatra*) *fragosa* Ehlers, 1887: 75, by subsequent designation of Hartman, 1959: 305. Gender: feminine.

Sarsonupis Fauchald, 1982a: 64. Type species: *Onuphis quadricuspis* M. Sars, in G.O. Sars, 1872: 407, by original designation.

Material examined. *Paradiopatra fragosa*—Caribbean: off Marquesas—juvenile SYNTYPES (MCZ 656); off Bahia Honda—2 SYNTYPES (MCZ 857); U.S.A.: Florida: off Sand Key—SYNTYPE (MCZ 766). *P. amoureuxi*—Africa: off Ivory Coast—2 (MNHP). *Onuphis lepta*—Panama—HOLOTYPE (USNM 19425). *Onuphis quadricuspis*—Norway: Drøbak, Oslofjord—5 PARALECTOTYPES (ZMO C3172); southwest—8 (AM W.198970); Bergen—2 (BMNH ZK 1921.5.1.1827).

Diagnosis. Tentacular cirri present; branchiae absent or with pectinate filaments; anterior hooks with long pointed hoods.

Definition. Prostomium (Fig. 22a) anteriorly rounded. Posterior antennae on anterior to median part of prostomium, with ceratophores with usually 3–5 (rarely up to 9) rings, sometimes indistinct or smooth, or with lateral projections; styles of antennae usually short to moderately long, rarely long, longest styles (usually posterior laterals) to setiger 3–9, rarely to 20. Frontal and labial palps oval, latter without distal lobes or median section (Fig. 22b). Nuchal grooves curved laterally, widely separated middorsally. Tentacular cirri inserted distally or subdistally on moderately long peristomium, peristomium with middorsal anterior fold, ventral lip with median section.

Anterior 3 (rarely 4–5) pairs of parapodia modified, not prolonged. Dorsal and ventral cirri long and digitiform (Fig. 22k), latter on anterior 2–4 (rarely 7–8) setigers; short transition zone of globular ventral cirri. Branchiae rarely absent, usually present from setiger 2–18, pectinate filaments; often restricted to anterior part of body (absent after setiger 30–50).

Hooks of modified parapodia uni- to tridentate (usually bidentate), pseudocompound with long, pointed hoods (Figs. 22c,d); shafts of hooks sometimes with 2 rows of minute spines (Fig. 20j). Pectinate setae (Fig. 22e) from setiger 2 or later, upper limbate setae (Fig. 22f) from setiger 1, lower limbate setae simple (Fig. 22g); bidentate hooded subacicular hooks (Fig. 22h) from setiger 9–28 (usually 9–10).

Jaws with mandibles, and maxillae (Fig. 22i) with distally slender Mx I, left Mx II sometimes with distal fang, moderately long Mx III, Mx V large, Mx VI

present or absent. Tubes with soft to tough inner parchment-like lining, often with thick outer layer of mud; other foreign particles may be attached at right angles, similar to *Diopatra* tubes.

Size. Usually small, length of most species less than 10 cm, width less than 2 mm.

Remarks. *Paradiopatra* was described as a subgenus of *Diopatra* for *D. (P.) fragosa* Ehlers, 1887 and *D. (P.) glutinatrix* Ehlers, 1887. The subgenus was characterized as *Diopatra*-like without branchiae. Hartman (1959)

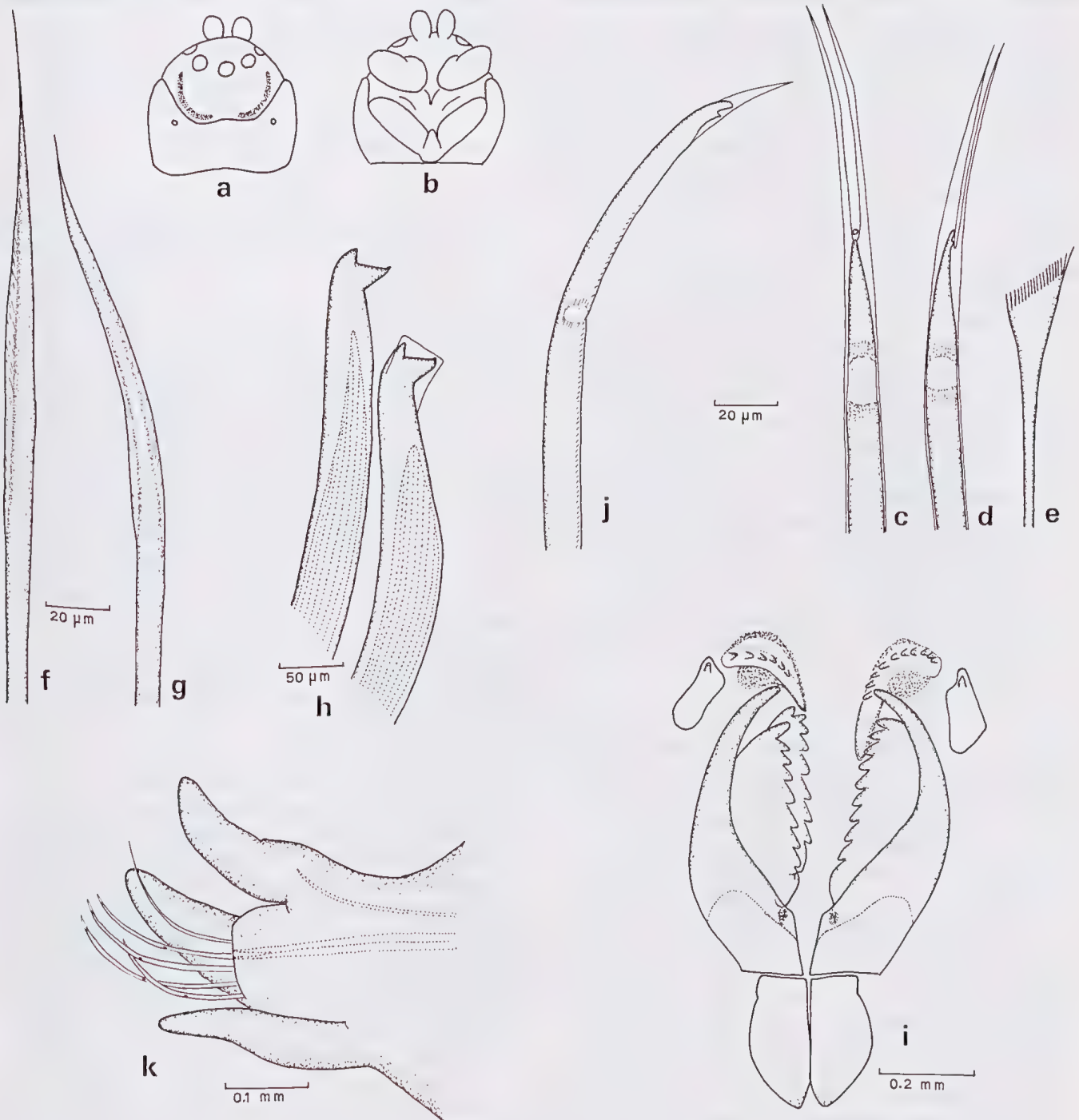


Fig. 22. *Paradiopatra quadricuspis* (AM W.198970): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, pseudocompound hook from setiger 1, frontal view; d, same, lateral view; e, pectinate seta from setiger 2 or later; f, upper limbate seta from setiger 1; g, lower limbate seta from setiger 1; h, subacicular hooks from setiger 21; i, maxillae. *P. fragosa* (syntype MCZ 766): j, pseudocompound hook from setiger 1; k, parapodium 1, anterior view.

designated *P. fragosa* the type species without giving reasons. Pettibone (1970) found the type specimens of *P. fragosa* in poor condition and considered the species doubtful. Although she stated that according to the original illustrations the two species appeared to belong to different genera, she overlooked Hartman's designation, designated *P. glutinatrix* the type species and redefined *Paradiopatra* on this basis as having two modified pairs of parapodia with specialized hooks, tentacular cirri, and branchiae present or absent. Fauchald (1982a) revised the genus, accepted *P. glutinatrix* as the type species and referred 10 more species from *Onuphis* to *Paradiopatra*.

Fauchald (1982a) examined the type specimens of *P. fragosa*. In addition to the two brittle syntypes, that were found unsatisfactory by Pettibone (1970), he located a third lot of syntypes in better condition. He stated, 'the types are certainly not in particularly good condition but they can be recognized and the additional original material makes it possible to characterize the species' and referred *P. fragosa* to the new genus *Sarsonuphis* (type species *Onuphis quadricuspis* M. Sars) which he described in the same paper.

The syntypes of *P. fragosa* were examined in the present study. The two lots of brittle syntypes appear to be adults and the third lot consists of juveniles of the same species. Since *P. fragosa* is the first designated type species of *Paradiopatra*, the name *Sarsonuphis* must be considered a junior synonym of the former genus, and the species referred to *Sarsonuphis* by Fauchald (1982a) are herewith referred to *Paradiopatra*.

The group of species referred to *Paradiopatra* by Pettibone (1970) and Fauchald (1982a) are referred to a new genus, *Anchinothria*, which is described above.

Fauchald (1982a) stated in the diagnosis of *Sarsonuphis* that large hooks were rarely present. The holotype of *P. lepta*, the only species for which he reported large hooks in setigers 4–9, was examined and no such hooks were found.

Onuphis (Onuphis) amoureuksi Intes & Le Loeuff, 1975 was considered by Fauchald (1982a) to resemble species of *Australonuphis* since it has similar presetal pockets. Glandular presetal pockets are found in several genera [e.g. *Rhamphobrachium*, *Onuphis* (see Fig. 6b)] and are not considered to be of generic importance. *Onuphis amoureuksi* has anterior pseudocompound hooks with long pointed hoods, and maxillae with distally slender Mx I, typical of the genus *Paradiopatra*. It is unusual, however, in being large (specimens examined measured 5–7 mm in width) and in having more digitiform ventral cirri and a later origin of subacicular hooks than other species of the genus. However, these differences may be due to its large size, and *O. amoureuksi* is herewith referred to *Paradiopatra*.

The following species are referred to *Paradiopatra*. This list is based on Fauchald (1982a), who gave a key to species (= *Sarsonuphis*): *Diopatra (Paradiopatra) fragosa* Ehlers, 1887; *Onuphis (Onuphis) amoureuksi* Intes & Le Loeuff, 1975; *Nothria armandi* McIntosh, 1885; *Onuphis bihanica* Intes & Le Loeuff, 1975 (? juvenile *P. amoureuksi*); *Nothria ehlersi* McIntosh, 1885;

Nothria fiordica Fauchald, 1974; *Onuphis furcatoseta* Monro, 1937; *Nothria hartmanae* Kirkegaard, 1980; *Nothria hispanica* Amoureux, 1972; *Onuphis (Onuphis) iberica* Hartmann-Schröder, 1975; *Onuphis lepta* Chamberlin, 1919; *Onuphis litabbranchia* Chamberlin, 1919; *Onuphis pachyctmema* Chamberlin, 1919; *Onuphis papillata* Kucheruk, 1979a; *Onuphis parva* Moore, 1911; *Diopatra paucibranchis* Ehlers, 1908; *Onuphis pauli* Annenkova, 1952; *Onuphis quadricuspis* M. Sars, 1872; *Onuphis socia* Chamberlin, 1919; *Onuphis parva striata* Uschakov, 1950; *Nothria willemoesii* McIntosh, 1885.

Distribution. World-wide, in 95–5270 m, most species deeper than 500 m (see Fauchald, 1982a).

Genus *Diopatra* Audouin & Milne Edwards

Figs 9b, 23a–1

Diopatra Audouin & Milne Edwards, 1833: 229. Type species: *Diopatra amboinensis* Audouin & Milne Edwards, 1833: 229, by subsequent designation of Malmgren, 1866: 180. Gender: feminine.

Material examined. *Diopatra aciculata*—**Australia:** Victoria: Port Phillip Bay—HOLOTYPE (NMV G1748); Western Australia: Bunbury—10 (AM W.5606) and others (WAM); South Australia—several (AM, SAM). *D. cuprea*—**U.S.A.:** North Carolina—10 (AHF n1642). *D. dentata*—**Australia:** New South Wales—1 (AM W.3826), 2 (AM W.198984) and others (AM). *D. heterodontata*—**Chile:** Punta Ronca—7 (ZMH P-13820). *D. monroi*—**South Africa:** Bay of Luderitz—1 (ZMH P-14284). *D. monroviensis*—**West Africa:** Monrovia—5 (ZMH V736-7). *D. musseraensis*—**Angola:** Mussera—HOLOTYPE (ZMH V907). *D. neapolitana*—**Italy:** Naples—4 (ZMH V10722). *D. ornata*—**U.S.A.:** California—many (AHF Velero sta. 5709-56). *D. rhizoicola*—**Peru:** San Lorenzo near Lima—PARATYPE (ZMH P15273). *D. spiribranchis*—**West Indies**—HOLOTYPE (ZMH PE-781). *D. n.sp. 1*—**U.S.A.:** Hawaii—10 (AM W.198985). *D. n.sp. 2*—**Australia:** Queensland—6 (AM W.198986) and others (AM, QM). *D. n.sp. 3*—**Australia:** New South Wales—2 (AM W.196435) and others (AM).

Diagnosis. Tentacular cirri present; branchial filaments arranged spirally around trunk.

Definition. Prostomium (Fig. 23a) anteriorly rounded to slightly extended. Posterior antennae on median part of prostomium, with ceratophores with 5–20 rings (sometimes with lateral projections), with moderately long to long styles. Frontal palps subulate; labial palps oval with distinct distal lobes and median section (Fig. 23b). Nuchal grooves rounded to almost circular, widely separated middorsally; tentacular cirri inserted distally on moderately long peristomium, middorsal part of peristomium with anterior fold; ventral lip with median section.

Anterior 3–5 (rarely 7) pairs of parapodia (Fig. 23c) modified, slightly prolonged; rarely with double postsetal lobes. Ventral cirri subulate on anterior 4–6 setigers, short transition zone of globular ventral cirri; dorsal cirri long to very long. Small ventral lobes on setiger 5–25 in some species. Branchiae from setiger 4–5,

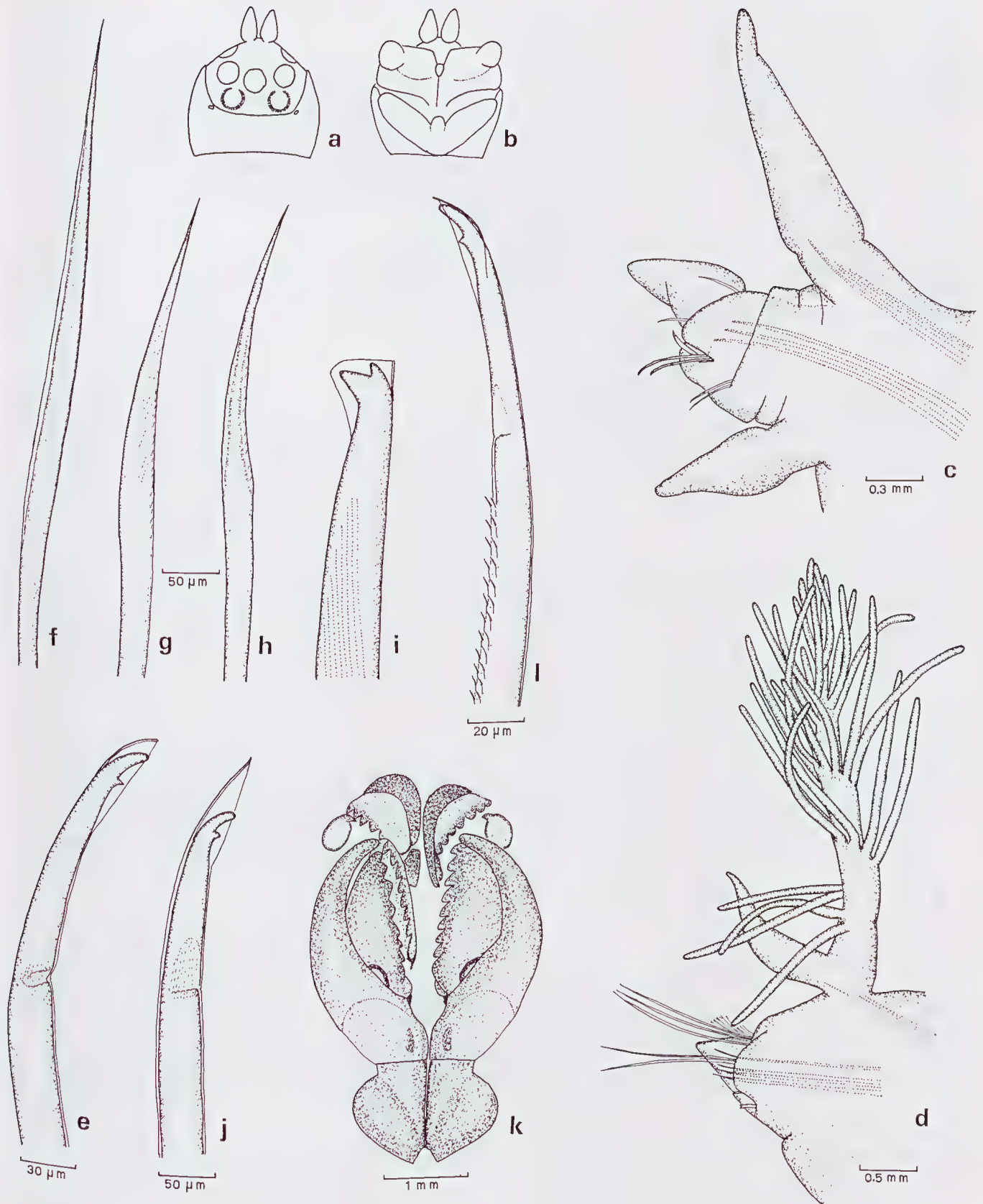


Fig. 23. *Diopatra cuprea* (AHF n1642): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, parapodium 1, anterior view; d, parapodium 38, same view; e, pseudocompound hook with short hood from setiger 1; f, upper limbate seta from setiger 21; g, lower cultriform limbate seta from same; h, lower spine-like limbate seta from setiger 36; i, subacicular hook from setiger 36. *D. aciculata* (AM W.5606): j, pseudocompound hook with long hood from setiger 36; k, maxillae. *D. heterodontata* (ZMH P-13820): l, pseudocompound spiny hook from setiger 2.

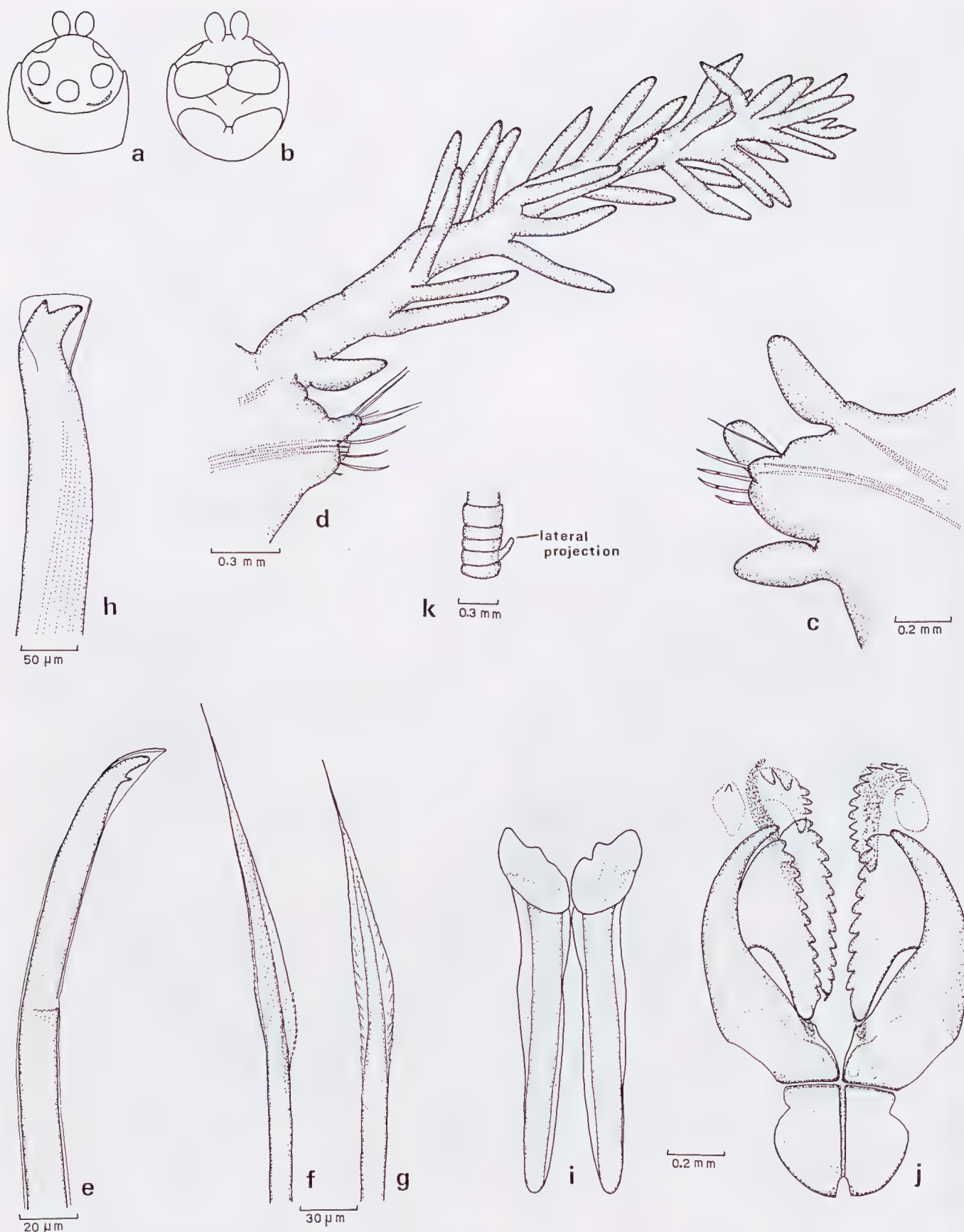


Fig. 24. *Epidiopatra hupferiana* (AM W.198962): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, parapodium 3, anterior view; d, parapodium 5, posterior view; e, pseudocompound hook from setiger 1; f, upper limbate seta from setiger 9; g, lower spine-like limbate seta from same; h, subacicular hook from setiger 29; i, mandibles; j, maxillae. *E. gilchristi* (paratype BMNH ZK 1963.1.85): k, ceratophore of left posterior lateral antenna.

filaments arranged spirally around trunk (Fig. 23d); well developed only on anterior part of body, single filaments from setiger 40–60.

Hooks of modified parapodia uni- to tridentate, pseudocompound with short (Fig. 23e) to long (Fig. 23j) hoods; shafts of hooks sometimes with 2 rows of minute spines (Figs 9a, 23l). Pectinate setae from setiger 5 or later, upper limbate setae (Fig. 23f) from setiger 1, lower limbate setae simple (Fig. 23g,h); bidentate hooded subacicular hooks (Fig. 23i) usually from setiger 15–20 (rarely 12–30).

Jaws with mandibles, and maxillae (Fig. 23k) with moderately long Mx III, Mx V large, Mx VI absent. Tubes robust, consisting of inner parchment-like layer and outer layer of foreign particles, often attached at right angle.

Size. Moderately large to large, length to 30 cm (250 setigers), width to 8 mm.

Remarks. Audouin & Milne Edwards (1833) did not designate a type species for *Diopatra*. The description of the genus was followed by that of *Diopatra amboinensis* with a note that *Nereis cuprea* delle Chiaje also belonged to the genus *Diopatra*. Milne Edwards (1838: 564) gave a short description of the genus and listed only one species, *Diopatra amboinensis*. This reference was taken as a type designation by Malmgren (1866) and stated as such. Hartman (1944) listed *Diopatra cuprea*, and Hartman (1959) *D. amboinensis* the type species, and either of the two designations have been followed by subsequent authors. The first author to unequivocally state the type species for the genus is Malmgren and his subsequent designation is herein accepted.

Although the genus *Diopatra* is well defined, the taxonomy is not clear at the specific level. Fauchald (1977) recognized 40 species. A complete revision of the genus is underway (Paxton, in preparation).

Distribution. In all major oceans, best represented in warmer waters; intertidal to shallow depths.

Genus *Epidiopatra* Augener

Fig. 24a–k

Epidiopatra Augener, 1918: 355. Type species: *Epidiopatra hupferiana* Augener, 1918: 355, by subsequent designation of Hartman, 1959: 300. Gender: feminine.

Material examined. *Epidiopatra hupferiana*—Australia: New South Wales—3 (ZMH V9570) and 3 (AM W.198962-3). *E. gilchristi*—South Africa—PARATYPE (BMNH ZK 1963.1.85).

Diagnosis. Tentacular cirri absent; branchial filaments arranged spirally around trunk.

Definition. Prostomium (Fig. 24a) anteriorly rounded. Posterior antennae on posterior part of prostomium, with ceratophores with 3–20 rings sometimes with lateral projections (Fig. 24k), with short to long posterior styles. Frontal and labial palps oval, latter without distal lobes, with small median section (Fig. 24b). Nuchal grooves slightly curved, with large

middorsal separation; peristomium moderately long, with middorsal anterior fold; ventral lip with small median section; tentacular cirri absent.

Anterior 3–4 pairs of parapodia (Fig. 24c) modified; not prolonged. Dorsal and ventral cirri digitiform, latter on anterior 3–5 setigers, short transition zone of globular ventral cirri. Branchiae from setiger 4–5, filaments arranged spirally around trunk (Fig. 24d); only on anterior part of body, last filaments from setiger 20–40.

Hooks of modified parapodia uni- to tridentate, pseudocompound with short to long hoods (Fig. 24e); shafts of hooks sometimes with 2 rows of minute spines. Pectinate setae from setiger 5 or later, upper limbate setae from setiger 1 (Fig. 24f), lower limbate setae simple (Fig. 24g); bidentate hooded subacicular hooks (Fig. 24h) from setiger 9–14.

Jaws with mandibles (Fig. 24i), and maxillae (Fig. 24j) with moderately long Mx III, Mx V large, Mx VI absent. Tubes consisting of tough inner parchment-like layer and outer layer of foreign particles, or only opaque tough substance with widely spaced rings (*E. gilchristi* and *E. tenuissima*).

Size. Small; length to 60 mm, width to 3 mm.

Remarks. Juvenile specimens of *Diopatra* have been confused with *Epidiopatra* and the validity of the latter genus has been questioned by Day (1960) and Intes & Le Loeuff (1975). The present study shows that species of *Epidiopatra* are not merely juveniles of *Diopatra* but represent a valid genus, possessing such neotenic and specialized features as the absence of tentacular cirri and the construction of opaque tough tubes respectively.

The following species are recognized: *E. hupferiana* Augener, 1918; *E. drewinensis* Augener, 1918; *E. gilchristi* Day, 1960; *E. papillosa* Day, 1967; *E. rugosa* Kucheruk, 1979a; *E. tenuissima* (Grube, 1868).

Distribution. Southern oceans: Africa, Australia; North Pacific: Japan; 20–1660 m.

Brevibrachium n. gen.

Figs 9a; 25a–k

Type species: *Rhamphobrachium capense* Day, 1960: 355. Gender: neuter.

Diagnosis. Anterior 3–5 pairs of parapodia prolonged, with more than 3 hooks each; hooks smooth, distally recurved, or uni- to tridentate with 2 rows of immoveable spines; setal sacs extending to setiger 4–8.

Definition. Prostomium anteriorly rounded. Posterior antennae on anterior to median part of prostomium, with ceratophores with 2–4 rings, with very short styles (to setiger 1). Frontal and labial palps oval, latter without distal lobes or median section (Fig. 25a). Nuchal grooves curved laterally, widely separated middorsally. Tentacular cirri inserted distally on short peristomium; peristomium with middorsal anterior fold; ventral lip without median section.

Anterior 3–5 pairs of parapodia modified (Fig. 25b,c),

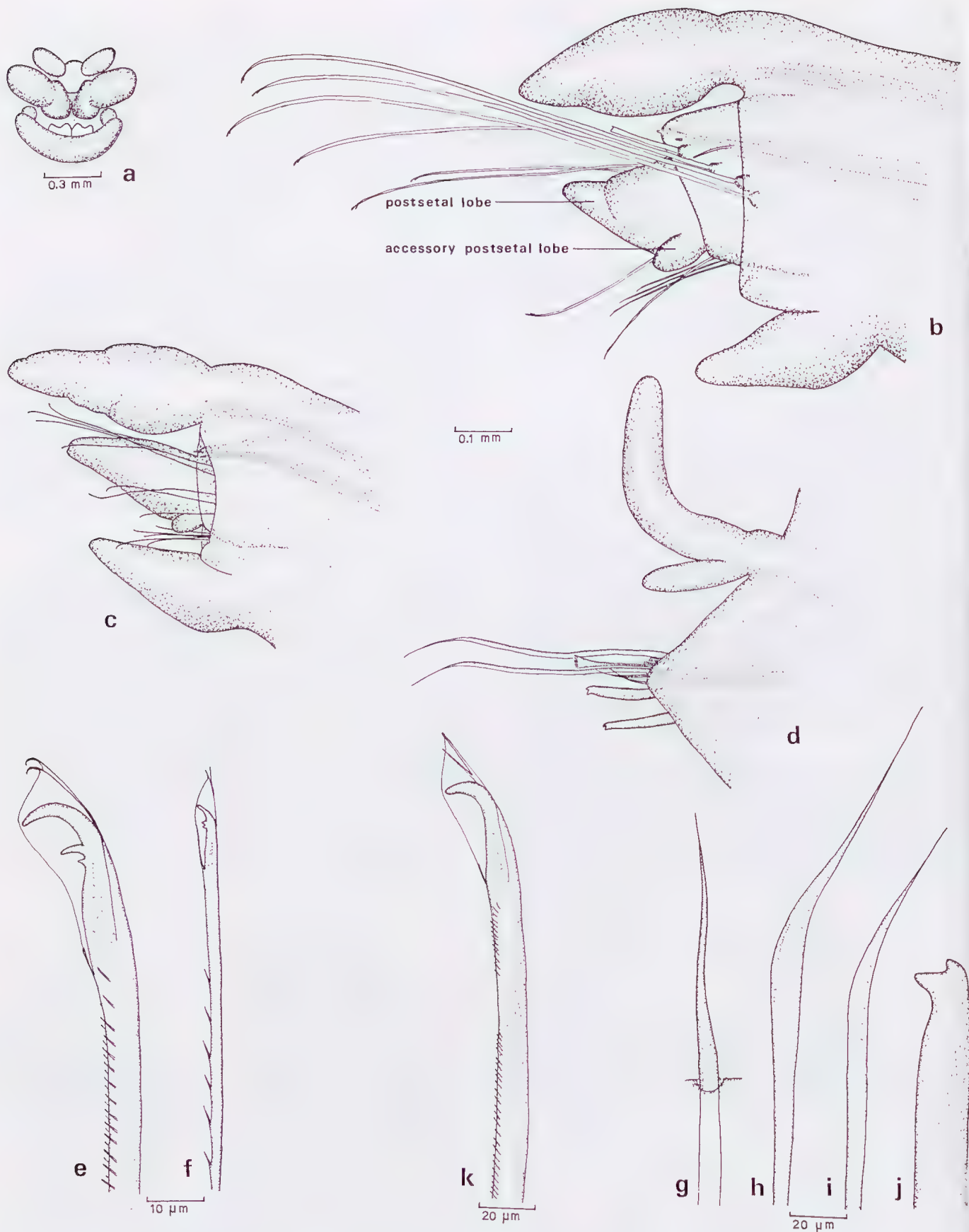


Fig. 25. *Brevibrachium capense* (a-j, paratype BMNH ZK 1961.20.4-7; k, paratype BMNH ZK 1961.20.14): a, prostomium and peristomium, ventral view; b, parapodium 1, anterior view; c, parapodium 4, anterior view; d, parapodium 60, posterior view; e, large tridentate spiny hook from setiger 1; f, small tridentate spiny hook from same; g, aciculum, from setiger 6; h, median limbate seta from same; i, lower limbate seta from same; j, subacicular hook from setiger 60; k, large unidentate spiny hook (number of setiger unknown).

moderately prolonged. Dorsal and ventral cirri subulate, latter on anterior 3–5 setigers, short transition zone of globular ventral cirri. Branchiae from setiger 2–40, single (Fig. 25d) or pectinate filaments.

Modified parapodia with more than 3 hooks each; hooks simple, smooth (Fig. 9a), recurved; or simple to pseudocompound, uni- to tridentate with hoods, shafts with 2 rows of immoveable spines (Fig. 25e,f,k); setal sacs of both types of hooks prolonged, extending to setiger 4–8 in body cavity. Internal capillary setae from setiger 1, pectinate setae from setiger 5 or later, limbate setae (Fig. 25h) from setiger 4–6, lower limbate setae (Fig. 25i) simple. Bidentate hooded subacicular hooks (Fig. 25j) from setiger 8–10.

Jaws with mandibles, and maxillae with moderately long Mx III, large Mx V, Mx VI absent. Tubes with mucous or parchment-like lining and outer layer of foreign particles; or burrows in limestone rock.

Size. Small; length to 42 mm (107 setigers), width to 2 mm.

Etymology. The name refers to the relatively short, modified parapodia; Latin *brevis* (short) and *brachium* (arm). The combination also emphasizes that *Brevibrachium*, *Longibrachium* and *Rhaphobrachium* are a group of related genera.

Remarks. *Brevibrachium* shares with *Rhaphobrachium* Ehlers, 1887 and *Longibrachium*, n. gen. the possession of modified parapodia with long setal sacs, and hooks with two rows of spines (spines in all but one species of *Brevibrachium*). These spines

are immoveable in *Brevibrachium* (when present) and *Longibrachium*, and moveable in *Rhaphobrachium*. *Brevibrachium* differs most markedly from *Longibrachium* in having relatively short modified parapodia with setal sacs extending to setiger 4–8, while those of *Longibrachium* are very long with setal sacs extending to setiger 20–60.

Three species, *Rhaphobrachium capense* Day, 1960, *R. maculatum* Estcourt, 1966 and a new species are referred to the new genus and described in Paxton (1986).

Distribution. Southern oceans: South Africa, Australia and New Zealand; intertidal to 90 m.

Longibrachium n. gen.

Figs 9c,d; 26a–e

Type species: *Rhaphobrachium atlanticum* Day, 1973: 55.
Gender: neuter.

Diagnosis. Anterior 4 pairs of parapodia prolonged, with more than 3 distally recurved hooks each; hooks with 2 rows of immoveable spines; setal sacs extending to setiger 20–60.

Definition. Prostomium (Fig. 26a) anteriorly rounded; posterior antennae on posterior part of prostomium, with ceratophores with 4–7 rings, with moderately long styles: longest style to setiger 6–15. Frontal palps globular; labial palps oval, without distal lobes, with median section (Fig. 26b). Nuchal grooves

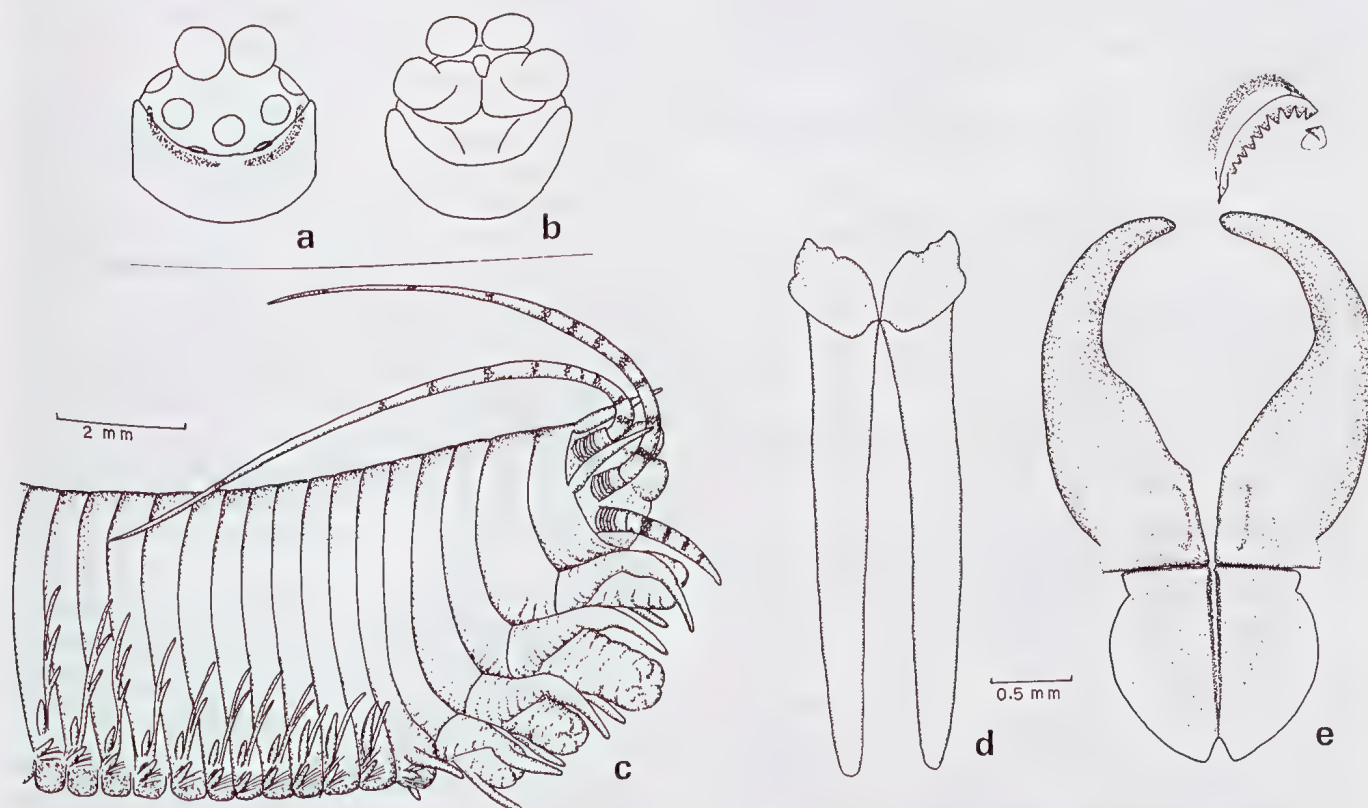


Fig. 26. *Longibrachium atlanticum* (holotype USNM 43124): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, anterior end, dorsolateral view; d, mandibles; e, part of maxillae.

straight, with small to large middorsal separation. Tentacular cirri inserted distally on moderately long peristomium; peristomium with middorsal anterior fold; ventral lip without median section.

Anterior 4 pairs of parapodia modified, moderately (Fig. 26c) to greatly prolonged. Dorsal cirri subulate and long on modified parapodia, later with basal swelling (rarely with basal process); ventral cirri subulate on anterior 4–5 setigers, short transition zone of globular ventral cirri. Small interramal papillae on setigers 7–12. Branchiae from setiger 6–7; pectinate filaments (maximum 6).

Modified parapodia with more than 3 hooks each; hooks simple, distally recurved, shafts with 2 rows of immoveable spines (Fig. 9c,d); setal sacs extending to setiger 20–60 in body cavity. Internal capillary setae from setiger 1, pectinate setae from setiger 5 or later, limbate setae from setiger 5, lower limbate setae simple. Bidentate hooded subacicular hooks from setiger 16–26.

Jaws with mandibles (Fig. 26d), and maxillae (Fig. 26e) with moderately long Mx III, Mx V small, Mx VI present or absent. Tubes with parchment-like inner lining and outer layer of foreign particles.

Size. Moderately large; length unknown, width to 6 mm.

Etymology. The name is suggested by the long anterior parapodia. Hence the Latin *longi* (long) and *brachium* (arm).

Remarks. The relationships of *Longibrachium* to *Brevibrachium* and *Rhamphobrachium* are discussed in 'Remarks' for *Brevibranchium*.

Three species, *Rhamphobrachium atlanticum* Day, 1973, *R. quadripes* Kucheruk, 1979 and a new species are referred to the new genus and described in Paxton (1986).

Distribution. Western North Atlantic, South Pacific, Gulf of Tonkin; 12–157 m.

Genus *Rhamphobrachium* Ehlers

Figs 9e,f; 27a–l

Rhamphobrachium Ehlers, 1887: 70. Type species: *Rhamphobrachium Agassizii* Ehlers, 1887: 70, by subsequent designation of Hartman, 1944: 47. Gender: neuter.

Paranorthia Moore, 1903: 448. Type species *Paranorthia brevicornuta* Moore, 1903: 448, by subsequent designation of Hartman, 1959: 306.

Diagnosis. Anterior 3 pairs of parapodia prolonged, with 3 distally recurved hooks each; hooks with 2 rows of moveable spines, setal sacs extending to setiger 30–60.

Definition. Prostomium (Fig. 27a) anteriorly rounded; posterior antennae on anterior to median part of prostomium, with ceratophores with 2–5 rings, with short styles (to setiger 2–5). Frontal palps globular; labial palps oval, without distal lobes, with distinct (Fig. 27b) to indistinct anterior median section. Nuchal grooves curved laterally, with small to large middorsal separation. Tentacular cirri inserted distally to

subdistally on moderately long peristomium, ventral lip without median section.

Anterior 3 pairs of parapodia modified, moderately prolonged. Dorsal and ventral cirri subulate, latter on anterior 3–4 setigers. Branchiae from setiger 6–17, single or pectinate filaments.

Modified parapodia with 3 long, simple to pseudocompound, distally recurved hooks (Fig. 27d,e) each, projecting from papilliform lobes; shafts with 2 rows of moveable spines (Fig. 9e,f); setal sacs extending to setiger 30–60 in body cavity. Internal capillary setae from setiger 1, pectinate and limbate setae (Fig. 27f,g) from setiger 4; lower limbate setae simple (Fig. 27h) to pseudocompound to compound (= spinigers). First 1–2 unmodified parapodia (Fig. 27c) rarely with falcigers. Bidentate hooded subacicular hooks (Fig. 27i,j) from setiger 10–16.

Jaws with mandibles (Fig. 27k), and maxillae (Fig. 27l) with moderately long Mx III, Mx V small to large, Mx VI present or absent. Tubes with parchment-like inner lining and outer layer of foreign particles.

Size. Small to large; length to 19+ cm (190+ setigers), width to 7 mm.

Remarks. *Rhamphobrachium* was erected by Ehlers (1887) for his previously described *Onuphis brevibrachiatum* and two new species, *R. chuni* and *R. agassizii*. The characteristics of the genus were given as three prolonged anterior pairs of parapodia with spiny, recurved hooks. This definition was later expanded by Monro (1937), Estcourt (1966) and Kucheruk (1979a) with the inclusion of species with two pairs of prolonged parapodia (*R. bipes*), with spineless recurved hooks (*R. maculatum*), and with four pairs of prolonged parapodia (*R. quadripes*).

The elucidation of *Rhamphobrachium* development (see p.18) has shown that specimens with two pairs of modified parapodia are juveniles. *Rhamphobrachium maculatum* and several species with four or five pairs of modified parapodia differ also in a number of additional important characters (types of spines, distal ends of setae, length of setal sacs, prostomial characters, etc.). These species represent different lineages from the genus *Rhamphobrachium* (type species *R. agassizii*) and are referred to two new genera *Brevibrachium* and *Longibrachium* described above. The definition of *Rhamphobrachium* is here restricted to species with 3 pairs of modified parapodia, each with 3 hooks with moveable spines, and long setal sacs (extending to setiger 30–60).

Moore (1903) described *Paranorthia* for his new species *P. brevicornuta*. He defined *Paranorthia* as intermediate between *Nothria* and *Rhamphobrachium* by possessing two pairs of prolonged parapodia, but lacking the long recurved setae. The holotype of *P. brevicornuta* has been examined in the present study. Although the setae of the modified parapodia are broken off, their internal long shafts are present and bear the two rows of moveable spines characteristic of the genus *Rhamphobrachium*. *Paranorthia brevicornuta*

was referred to *Rhamphobrachium* by Kucheruk (1979: 119), and *Paranorthia* considered a junior synonym of the latter genus, a decision that is supported by the present study.

A complete revision of *Rhamphobrachium*, providing a key to and descriptions of the 12 currently recognized species is published separately (Paxton, 1986).

Distribution. World-wide; intertidal to 2165 m.

Genus *Americonuphis* Fauchald

Figs 28a–d, 29a–e

Americonuphis Fauchald, 1973: 22. Type species: *Diopatra magna* Andrews, 1891b: 286, by original designation. Gender: feminine.

Material examined. *Americonuphis magna*—U.S.A.: North Carolina—2 (AM W.198971-2). *A. reesei*—Panama: Gulf of Panama—HOLOTYPE (AHF Poly 0729); Naos Island—1 (AHF).

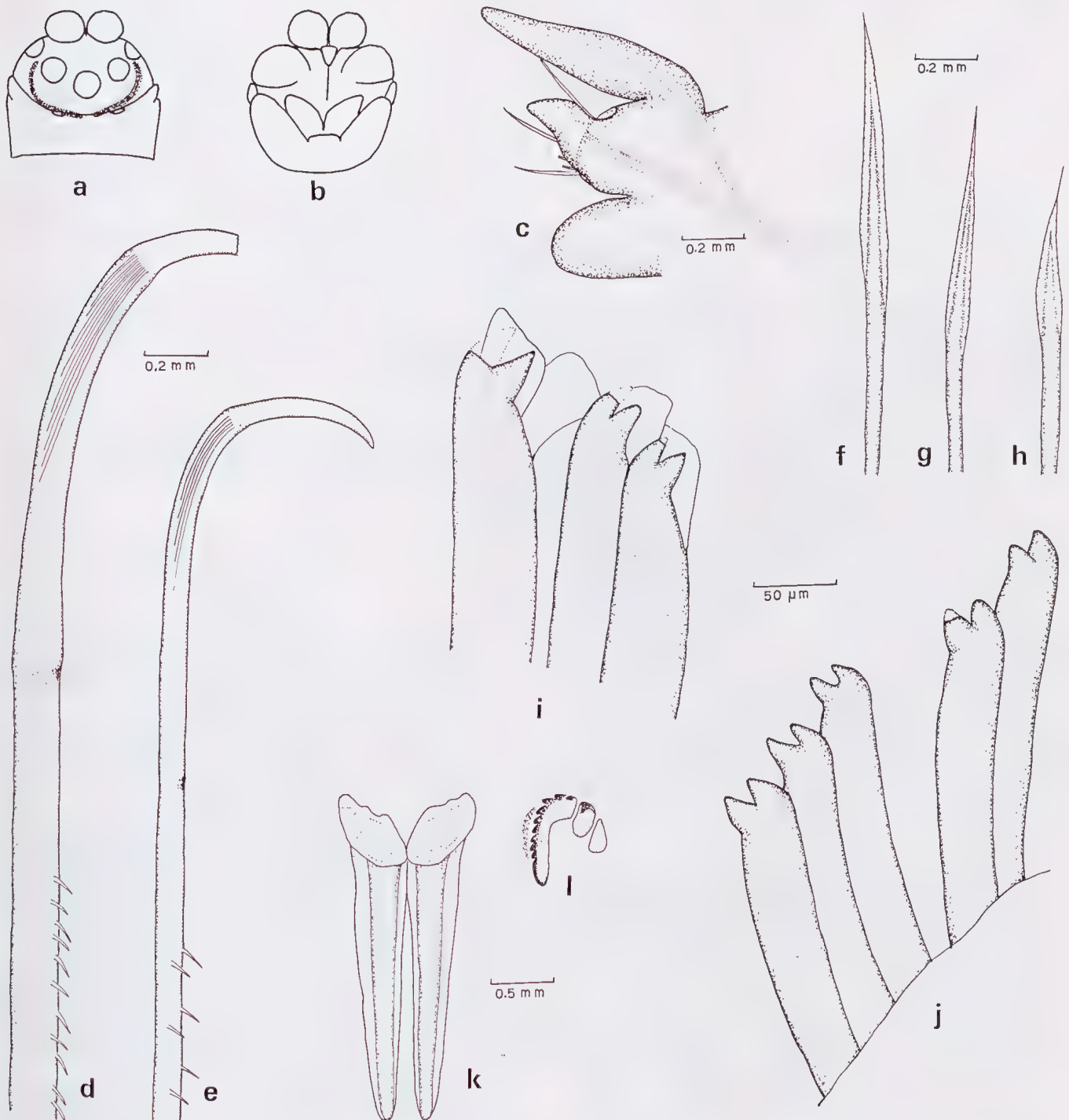


Fig. 27. *R. (Rhamphobrachium) agassizii* (c, e, f–h, j, USNM 20070; d, i, k, l, lectotype MCZ 789): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, parapodium 4, posterior view; d, recurved hook (tip broken) from parapodium I of lectotype; e, same from specimen from Puerto Rico; f, upper limbate seta from setiger 13; g, median limbateseta from same; h, lower spine-like limbate seta from same; i, subacicular hooks from setiger 17 of lectotype; j, same from setiger 19 of specimen from Puerto Rico; k, mandibles; l, right Mx IV, V and VI.

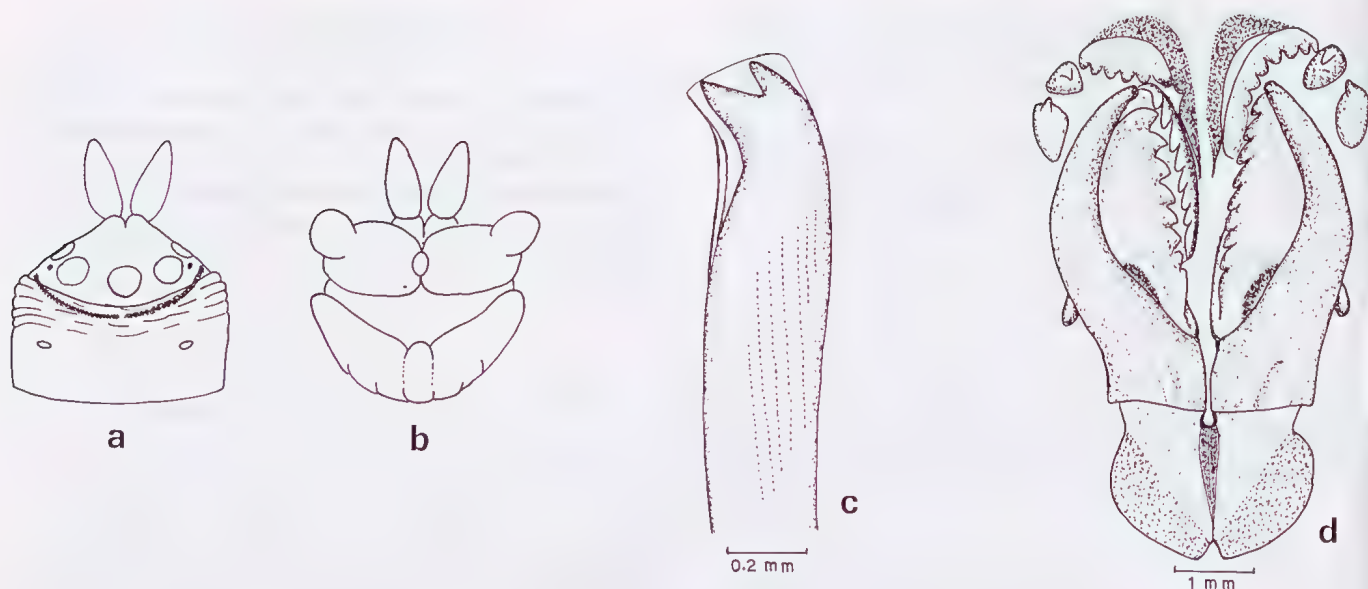


Fig. 28. *Americonuphis magna* (AM W.198971): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, subacicular hook from setiger 95; d, maxillae.

Diagnosis. Tentacular cirri inserted in middle of expansible peristomium; modified parapodia directed strongly anteroventrally, ventral cirri of setiger 5 almost touching in ventral midline.

Definition. Prostomium (Fig. 28a) very short, weakly incised and anteriorly extended. Posterior antennae on posterior part of prostomium, with ceratophores with 5–8 rings, and with short to moderately long styles: longest style (median) to setiger 4–9. Frontal palps subulate; labial palps oval with distinct distal lobes and median section (Fig. 28b). Nuchal grooves straight, with small middorsal separation, covered by anterior folds of expansible peristomium; tentacular cirri inserted in middle of moderately long peristomium; ventral lip with median section.

Anterior 3–5 pairs of parapodia (Fig. 29b) modified, slightly prolonged, directed strongly anteroventrally, ventral cirri of setiger 5 almost touching in ventral midline (Fig. 29a); dorsal and ventral cirri subulate, latter on anterior 4–5 setigers. Branchiae (Fig. 29d) from setiger 6; thick stem, pectinate filaments (maximum 7–12).

Hooks of modified parapodia bidentate, pseudocompound with hoods (Fig. 29c). Pectinate setae (Fig. 29e) from setiger 5 or later, upper limbate setae from setiger 1, lower limbate setae simple; bidentate hooded subacicular hoods (Fig. 28c) from setiger 16–18.

Jaws with mandibles, and maxillae (Fig. 28d) with moderately long Mx III, Mx V moderately large, Mx VI present. Tubes consisting of inner parchment-like lining and outer layer of foreign particles.

Size. Large; length to 73 cm, width to 10 mm.

Remarks. The following species are recognized: *A. magna* (Andrews, 1891); *A. reesei* Fauchald, 1973.

Distribution. Western North Atlantic Ocean: Gulf of Mexico, Caribbean; intertidal to 45 m.

Key to Species of *Americonuphis*

- Anterior part of body with brown pigment spots; maximum of 12 filaments per branchia. *A. magna*
- Anterior part of body without pigment spots; maximum of 7 filaments per branchia (Fig. 29d). *A. reesei*

Genus *Australonuphis* Paxton

Fig. 30a–l

Americonuphis Orensanz, 1974: 100. Type species *Americonuphis casamiquelorum* Orensanz, 1974, by original designation (preoccupied by *Americonuphis* Fauchald, 1973).

Australonuphis Paxton, 1979: 270. Type species: *Americonuphis casamiquelorum* Orensanz, 1974, by original designation (replacement name for *Americonuphis* Orensanz, 1974). Gender: feminine.

Material examined. *Diopatra teres*—Australia: New South Wales—HOLOTYPE (ZMB 6727). *Australonuphis teres*—Australia: New South Wales—8 (AM W.16051) and others. *A. parateres*—Australia: New South Wales: Narrabeen near Sydney—HOLOTYPE (AM W.11798), 5 PARATYPES (AM W.15069–73) and others (AM); Queensland—many (AM W.16550) and others.

Diagnosis. Antennae with moderately long ceratophores (about 10 rings) and short styles; anterior hooks uni- to weakly bidentate; distally entire subacicular hooks from setiger 50–80.

Definition. Prostomium (Fig. 30a) anteriorly rounded. Posterior antennae almost covering dorsal part of very short prostomium (Fig. 30b), with ceratophores with about 10 rings and short styles: longest style (median) to setiger 3–4, anterior lateral styles as long as their ceratophores. Frontal and labial palps oval,

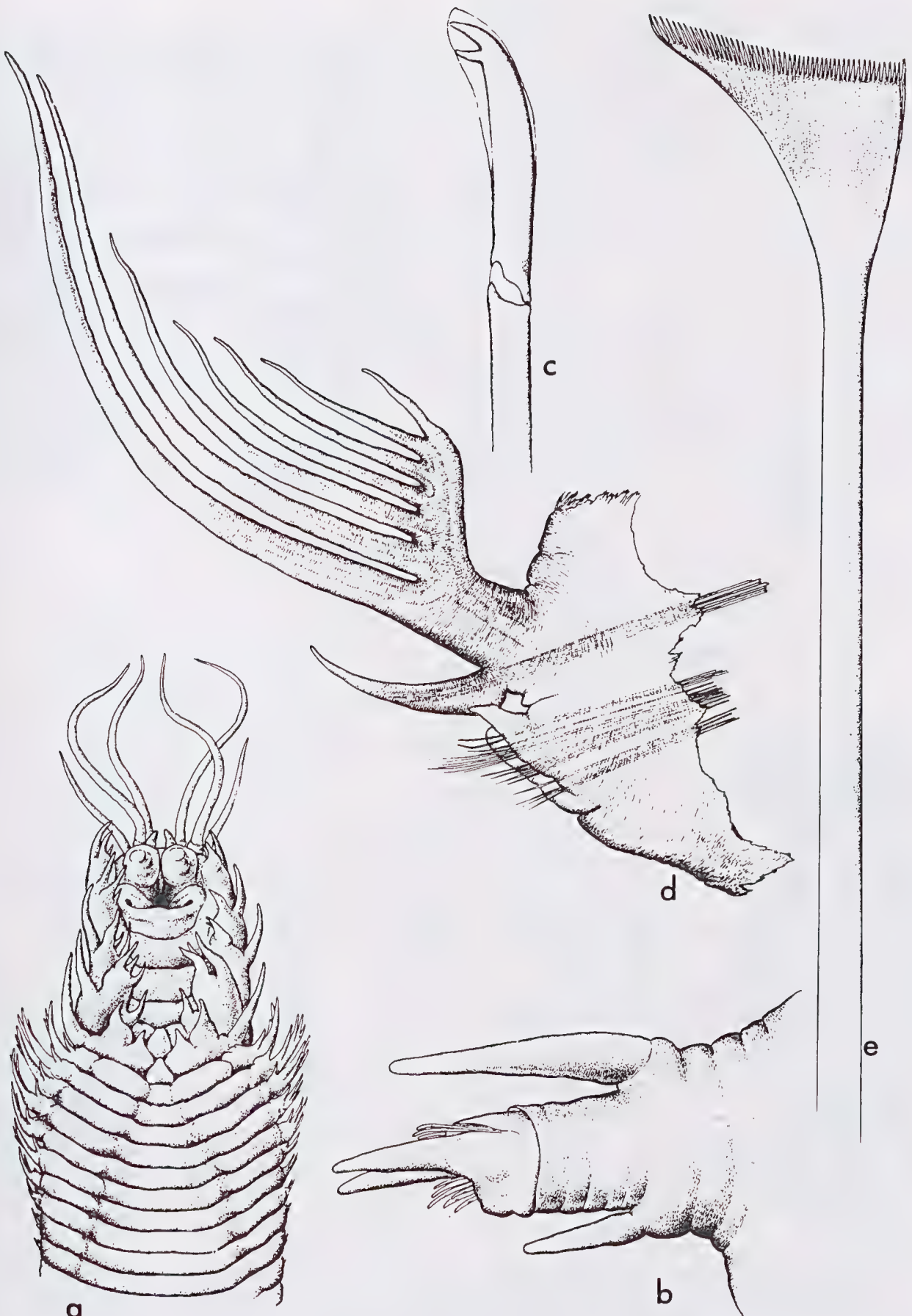


Fig. 29. *Americonuphis reesei* (from Fauchald, 1973: fig. 3a-e): a, anterior end, ventral view; b, parapodium 1, posterior view; c, pseudocompound hook from setiger 1; d, branchial parapodium, posterior view; e, pectinate seta.

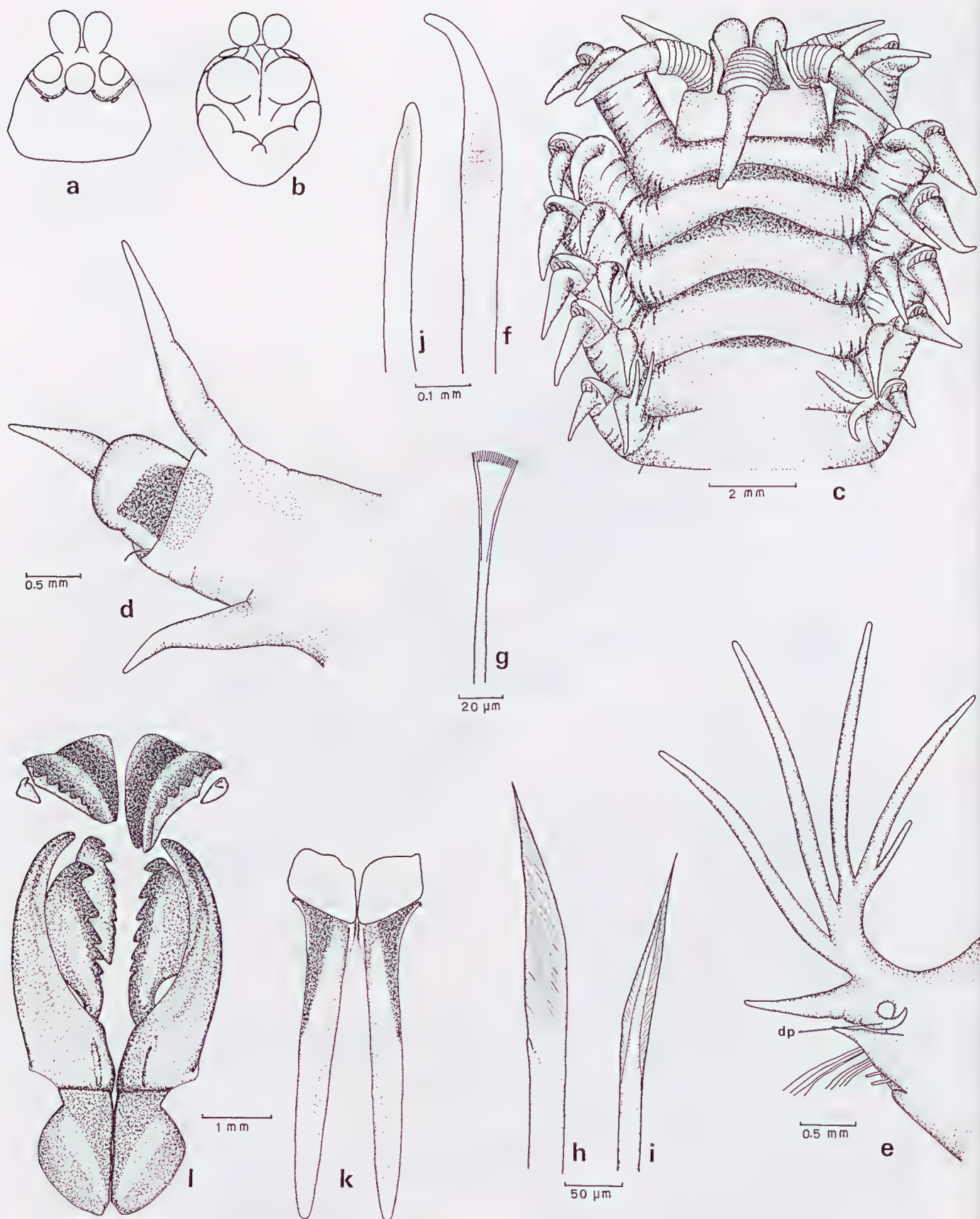


Fig. 30. *Australonuphis parateres* (c-j from Paxton, 1979: figs 9, 10-12, 15, 16): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, anterior end, dorsal view; d, parapodium 1, anterior view; e, parapodium 84, posterior view (dp = digital process); f, pseudocompound hook from setiger 1; g, pectinate seta from setiger 84; h, weakly pseudocompound cultriform limbate seta from setiger 17; i, spine-like limbate seta from setiger 65; j, subacicular hook from setiger 84. *Australonuphis teres* (from Paxton, 1979: figs 6, 7): k, mandibles; l, maxillae (Mx III to Mx V not in natural position).

latter without median section. Nuchal grooves widely separated in midline, curved towards base of median antenna. Tentacular cirri inserted distally on moderately long to long peristomium; middorsal part of peristomium without distinct anterior fold, appearing to extend along nuchal grooves to median antenna, ventral lip with indistinct median section.

Anterior 5–8 pairs of parapodia modified, moderately prolonged (parapodia 2–4 longest) (Fig. 30c,d). Ventral cirri subulate on anterior 6–8 setigers, long transition zone of glandular pads with reduced cirri (until setigers 15–25). Dorsal cirri moderately long, with basal swelling from setiger 6–7, gradually developing into digital process (Fig. 30e). Interramal papilla from setiger 6–7, moving ventrally, forming new presetal lip by setiger 15–20, and fusing with ventral pad by setiger 40–70. Branchiae from setiger 6 with thick stem and pectinate filaments (maximum of 6–7).

Hooks of modified parapodia uni- to weakly bidentate, pseudocompound without hoods (Fig. 30f); large median hooks absent. Pectinate setae (Fig. 30g)

from setiger 6–7; upper limbate setae from setiger 1; lower limbate setae weakly pseudocompound, cultriform (Fig. 30h) to simple, spine-like (Fig. 30i). Distally entire subacicular hooks without hood (Fig. 30j) from setiger 50–80.

Jaws with strongly sclerotized mandibles (Fig. 30k), and maxillae (Fig. 30l) with short Mx III, small Mx V, Mx VI absent. Tubes thin and temporary, consisting of inner mucous and outer layer of sand.

Size. Large; length of live worms to 300 cm, width to 2.5 cm; preserved to 70 cm long (1065 setigers); 10 mm wide.

Remarks. The following species are recognized: *A. casamiquelorum* (Orensanz, 1974); *A. hartmanae* (Friedrich, 1956); *A. parateres* Paxton, 1979; *A. teres* (Ehlers, 1868); *A. violacea* Rozbaczylo & Castilla, 1981.

Distribution. Pacific Ocean: eastern Australia, El Salvador, Chile; Atlantic Ocean: Brazil and Argentina; intertidal to 14 m.

Key to Species of *Australonuphis*

1. Five anterior setigers with weakly bidentate pseudocompound hooks. 2
 - Six to eight anterior setigers with unidentate pseudocompound hooks (Fig. 30f). 3
2. Peristomium and modified segments dark blue-violet; pseudocompound hooks distally curved and blunt. *A. violacea*
 - Peristomium and modified segments grayish-green; pseudocompound hooks distally less curved and pointed. *A. casamiquelorum*
3. Seven to eight anterior setigers with pseudocompound hooks. *A. hartmanae*
 - Six anterior setigers with pseudocompound hooks. 4
4. Brown transverse bands after setiger 8; frontal palps at least partly brown. *A. teres*
 - No brown bands after setiger 8; frontal palps white. *A. parateres*

Hartmanonuphis n. gen.

Fig. 31a–i

Type species: *Onuphis pectinata* Knox & Hicks, 1973: 289.
Gender: feminine.

Material examined. *Onuphis pectinata*—New Zealand: Timaru—HOLOTYPE (CM); Banks Peninsula—2 PARATYPES (CM). *Hartmanonuphis pectinata*—New Zealand: Kaitaia—2 (AM W.198977) and 1 (USNM 98883).

Diagnosis. Antennae with short ceratophores (6–8 rings) and moderately long styles; short anterior dorsal cirri; long transition zone of ventral glandular pads with reduced cirri (until setiger 14–16); anterior hooks bidentate; bidentate subacicular hooks from setiger 29–31.

Definition. Prostomium (Fig. 31a) with anterior median incision. Posterior antennae almost covering

dorsal part of short prostomium, with ceratophores with 6–8 rings, and short styles: longest styles (posterior laterals) to setiger 3–5, anterior lateral styles shorter than their ceratophores. Frontal and labial palps oval, latter without median section (Fig. 31b). Nuchal grooves widely separated in midline, curved towards base of median antenna. Tentacular cirri inserted distally on moderately long peristomium. Middorsal part of peristomium without distinct anterior fold, appearing to extend along nuchal grooves to median antenna; ventral lip with distinct median section.

Anterior 6 pairs of parapodia modified, moderately prolonged (parapodia 2–4 longest) (Fig. 31c). Ventral cirri subulate on anterior 6 setigers, long transition zone of glandular pads with reduced cirri (until setiger 14–16) (Fig. 31d). Dorsal cirri moderately long, with basal swelling. Ventral lobe from setiger 9–12, enlarging

dorsally and forming new presetal lip by setiger 25. Branchiae from setiger 1, with thick stem and pectinate filaments (maximum 9–11).

Hooks of modified parapodia bidentate, pseudocompound with hoods (Fig. 31e); large median hooks absent. Pectinate setae (Fig. 31f) from setiger 2; upper limbate setae from setiger 1, lower limbate setae simple; bidentate hooded subacicular hooks (Fig. 31g) from setiger 29–31.

Jaws with strongly sclerotized mandibles (Fig. 31h), and maxillae (Fig. 31i) with short Mx III, small Mx V, Mx VI absent. Tubes thin and temporary, consisting of inner mucous and thin outer layer of sand.

Size. Large; width 3.5 to 8 mm; length to 50 cm (800 setigers).

Etymology. Named in honour of Dr Olga Hartman, who has introduced and encouraged me to the study of polychaetes.

Remarks. The new genus is closest to *Australonuphis* and *Hirsutonuphis* (described below) with which it shares the prolonged anterior parapodia and curved nuchal grooves. It differs mainly from *Australonuphis* by having bidentate, pseudocompound and subacicular hooks instead of distally entire hooks, and from *Hirsutonuphis* by having shorter dorsal cirri, shorter

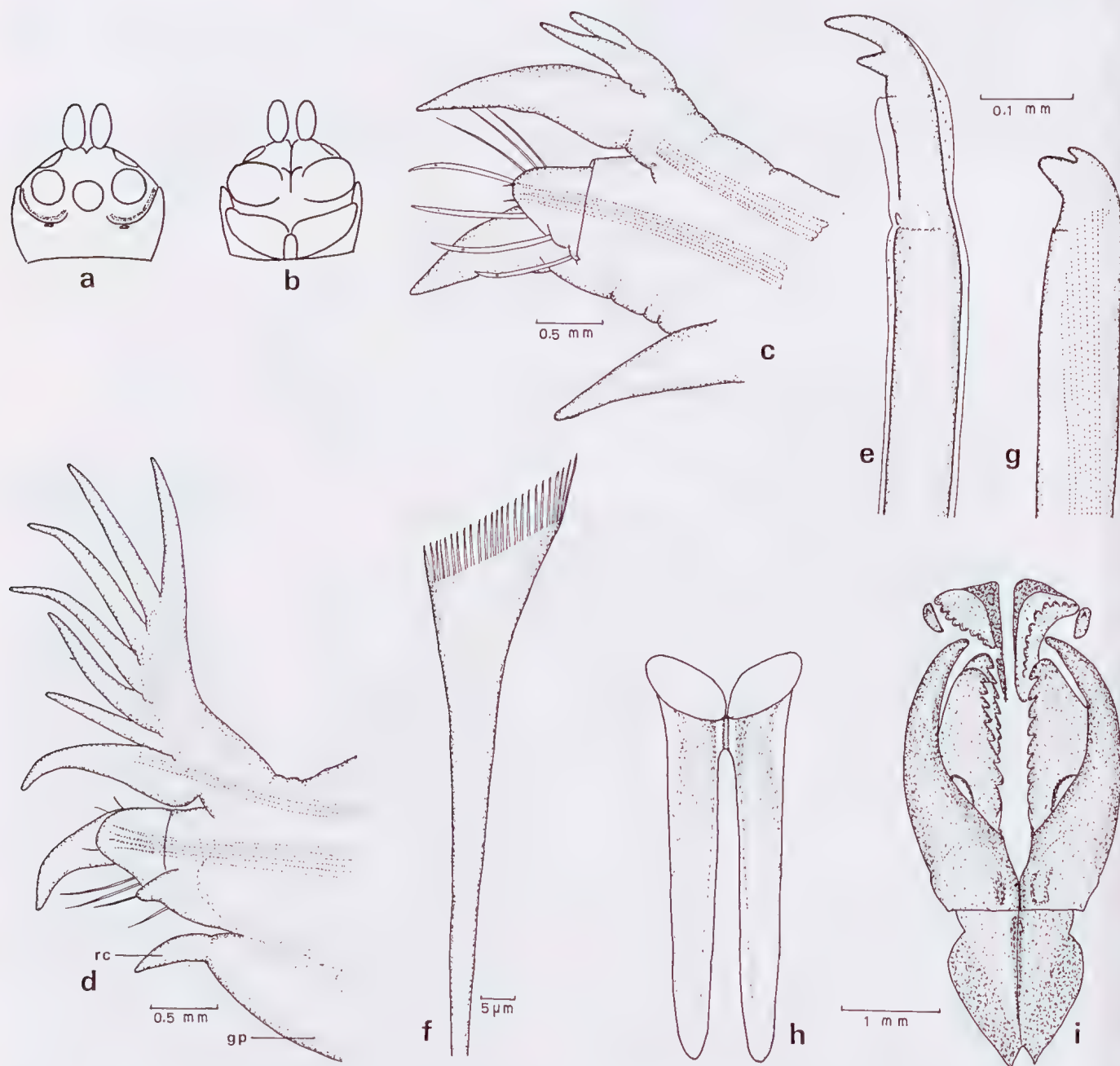


Fig. 31. *Hartmanonuphis pectinata* (a–d, f, h, i, AM W.198977; e, g, paratype, CM): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, parapodium 1, anterior view; d, parapodium 12, anterior view (gp = glandular pad; rc = reduced cirrus); e, pseudocompound hook from setiger 2; f, pectinate seta from setiger 200; g, subacicular hook from setiger 50; h, mandibles; i, maxillae.

ceratophores and uniformly sclerotized, instead of the characteristically sclerotized, maxillary carriers.

The type specimens of *O. pectinata*, the only known species in the genus, were examined. The modified parapodia contain 3–4 upper limbate setae instead of 12 as described by Knox & Hicks (1973).

Distribution. South Pacific Ocean: New Zealand; intertidal to 85 m.

Hirsutonuphis n. gen.

Fig. 32a–l

Type species: *Onuphis mariahirsuta* Paxton, 1979: 277.

Gender: feminine.

Material examined. *Onuphis mariahirsuta*—Australia: New South Wales: Coffs Harbour—HOLOTYPE (AM W.11799), 5 PARATYPES (AM W.15083–7) and others (AM). *Onuphis geminata*—Central America: Belize—2 PARATYPES (USNM 061240). *Onuphis gygis*—Australia: Queensland: Fraser Island—HOLOTYPE (AM W.15103) and 2 PARATYPES (AM W.15104–5). *Onuphis zebra*—Mexico: Lower California: Punta Gorda—HOLOTYPE (USNM 32898). *Hirsutonuphis* n. sp. 1—Australia: New South Wales: Botany Bay near Sydney—2 (AM W.13768), 2 (AM W. 13775) and others (AM); Queensland—several (AM). *H. n.sp.* 2—Australia: New South Wales—1 (AM W.6258), 2 (AM W.6263) and others (AM).

Diagnosis. Antennae with moderately long ceratophores (10–15 rings) and moderately long styles; long to very long anterior dorsal cirri; maxillary carriers with darkly sclerotized median part and lateral triangles.

Definition. Prostomium (Fig. 32a) with anterior median incision. Posterior antennae almost covering dorsal part of short prostomium, with ceratophores with 10–15 rings and moderately long styles: longest styles (posterior laterals) to setiger 4–10, anterior lateral styles shorter to longer than their ceratophores. Frontal palps oval; labial palps oval to rectangular, with or without median section (Fig. 32b). Nuchal grooves widely separated in midline, curved towards base of median antenna. Tentacular cirri inserted distally on short to moderately long peristomium. Middorsal part of peristomium without distinct anterior fold, appearing to extend along nuchal grooves to median antenna; ventral lip with median section.

Anterior 5–8 pairs of parapodia modified, moderately

prolonged (parapodia 2–4 longest) (Fig. 32j). Ventral cirri subulate on anterior 6–8 setigers, short transition zone of glandular pads with reduced cirri (until setiger 9–11). Dorsal cirri long to very long (Fig. 32c,j) with basal swelling (Fig. 32d). Interramal papilla on setigers 11–18 in *H. zebra*. Branchiae usually from setiger 6 (rarely 8–9), with thick stem and pectinate filaments (maximum of 8–12).

Hooks of modified parapodia bi- to tridentate, pseudocompound with hoods (Fig. 32e,f); median hooks usually slightly larger but not becoming simple or remaining into unmodified parapodia. Pectinate (Fig. 32k,l) and upper limbate setae from setiger 1, lower limbate setae simple; bidentate hooded subacicular hooks (Fig. 32g) usually from setiger 20–30 (rarely 15 to after 35).

Jaws with mandibles (Fig. 32h), and maxillae (Fig. 32i) with moderately long Mx III, short Mx V, Mx VI absent. Carriers heart-shaped; lateral triangular area between Mx I and carriers, and anterior median region of carriers strongly sclerotized. Tubes thin, temporary, consisting of inner mucous and outer layer of sand.

Size. Small to large; width 1.1 to 6 mm; longest complete specimen (type species) measures 56 cm for 1040 setigers.

Etymology. The modified parapodia with their long dorsal cirri give the animals a 'hairy' appearance, hence the first part of the name. This is combined with *Onuphis*, the first described genus in the family.

Remarks. *Hirsutonuphis* is the only onuphid genus that has diagnostic maxillary carriers. It is most closely related to *Hartmanonuphis*, which has been described above and their relationships discussed.

The holotype of *O. zebra* was examined and found to contain no compound spinigers, contrary to Fauchald (1980; 1982a).

The following species are referred to *Hirsutonuphis*: *Onuphis mariahirsuta* Paxton, 1979; *Onuphis acapulcensis* Rioja, 1944; *Onuphis (Onuphis) geminata* Fauchald, 1980; *Onuphis gygis* Paxton, 1979; *Onuphis zebra* Berkeley & Berkeley, 1939; *H. n.sp.* 1; *H. n.sp.* 2.

Distribution. Pacific Ocean: eastern Australia, Guatemala, Mexico; Atlantic Ocean: Caribbean Sea; intertidal to 36 m.

Key to Described Species of *Hirsutonuphis*

1. Anterior dorsal cirri as thick as antennae (Fig. 32j); pseudocompound hooks of anterior setigers bidentate. *H. gygis*
- Anterior dorsal cirri much thinner than antenna (Fig. 32c); pseudocompound hooks of anterior setigers bi- to tridentate (Fig. 32e,f). 2
2. Conical interrarmal papilla on setigers 11–18; subacicular hooks after setiger 35. *H. zebra*
- Interramal papilla absent; subacicular hooks from setiger 15–26. 3

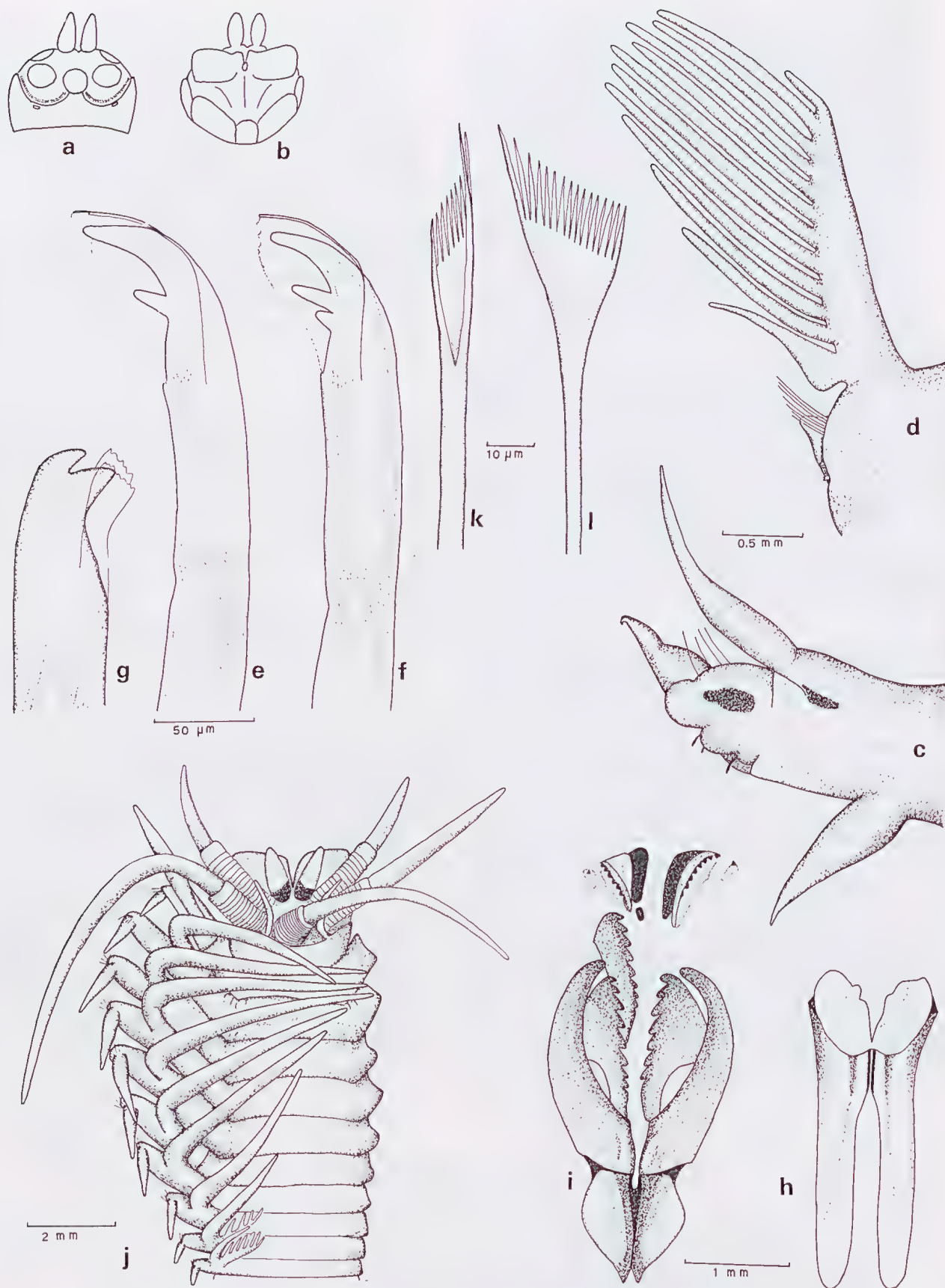


Fig. 32. *Hirsutonuphis mariahirsuta* (c–i from Paxton, 1979: figs 24, 26, 27, 29, 31–33): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, parapodium 1, anterior view; d, parapodium 60, same view; e, bidentate pseudocompound hook from setiger 1; f, tridentate pseudocompound hook from same; g, subacicular hook from setiger 60; h, mandibles; i, maxillae (Mx III to Mx V not in natural position). *H. gygis* (from Paxton, 1979: figs 34, 38, 39): j, anterior end, dorsal view; k, rolled up pectinate seta from setiger 1; l, flat pectinate seta from median region.

3. Subacicular hooks from setiger 15–18; all pseudocompound hooks tridentate.
 *H. acapulcensis*
- Subacicular hooks from setiger 20–26; pseudocompound hooks bi- and tridentate. 4.
4. No brown middorsal bands (Fig. 32j) after setiger 6. *H. mariahirsuta*
- Brown middorsal bands from setiger 2–50. *H. geminata*

Genus *Aponuphis* Kucheruk

Fig. 33a–h

Aponuphis Kucheruk, 1978: 91. Type species: *Hyalinoecia bilineata* Baird, 1870: 358, by original designation. Gender: feminine.

Material examined. *Hyalinoecia bilineata*—U.K.: off Cornwall—3 SYNTYPES (BMNH ZH 1867.1.7.2). *Aponuphis bilineata*—Ireland: off Cork—1 (BMNH ZB 1983.314).

Diagnosis. Antennae with moderately long to long ceratophores (10–20 rings); branchiae absent or as single filaments; tentacular cirri absent.

Definition. Prostomium (Fig. 33a) anteriorly extended. Posterior antennae on median to posterior

part of prostomium, with ceratophores with 10–20 rings and moderately long to long styles (to setigers 8–20), anterior lateral styles shorter to longer than their ceratophores. Frontal palps oval; labial palps rectangular without median section (Fig. 33b). Nuchal grooves straight, small middorsal separation. Tentacular cirri absent. Peristomium moderately long, middorsal part of peristomium with anterior fold; ventral lip with weakly defined median section.

Anterior 5 pairs of parapodia (Fig. 33c) modified, not prolonged. Ventral cirri subulate on anterior 5–7 setigers, short transition zone of globular ventral cirri; dorsal cirri moderately long. Branchiae, rarely absent, usually present from setiger 4, rarely 1–7; single filament.

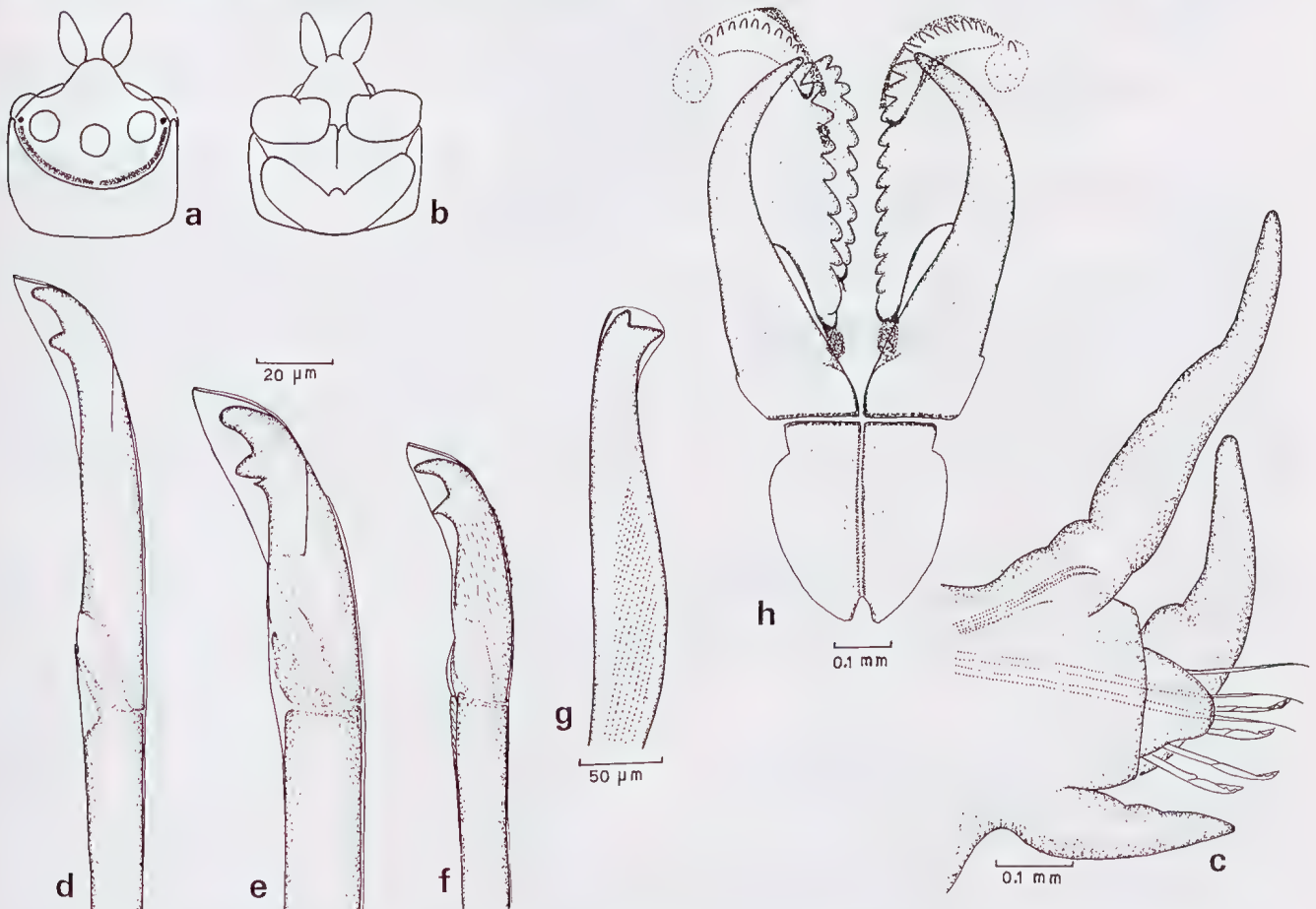


Fig. 33. *Aponuphis bilineata* (c, f, syntype BMNH ZH 1867.1.7.2; d, e, g, h, BMNH ZK 1983.314): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, parapodium 1, anterior view; d, lower bidentate pseudocompound hook from setiger 1; e, median tridentate pseudocompound hook from setiger 1; f, lower bidentate pseudocompound hook from setiger 5; g, subacicular hook from posterior setiger; h, maxillae.

Hooks of modified parapodia bi- to tridentate, pseudocompound with hoods (Fig. 33d-f); median hooks slightly larger, remaining to setiger 7 but not becoming simple. Pectinate setae from setiger 6-7; upper limbate setae from setiger 1, lower limbate setae simple; bidentate hooded subacicular hooks (Fig. 33g) from setiger 8-20.

Jaws with mandibles, and maxillae (Fig. 33h) with moderately long Mx III, large Mx V, Mx VI absent. Tubes thin, consisting of inner mucous and outer layer of sand or broken shells.

Size. Small; length to 80 mm (250 setigers), width less than 1.5 mm.

Remarks. Bellan (1964) considered all subspecies and related species of *A. bilineata* as ecological 'forms' and synonyms of that species. In view of the differences involved, this judgement appears very conservative, and the species are retained until more conclusive evidence of their conspecificity is available.

The following species are recognized: *A. bilineata* (Baird, 1870); *A. brementi* (Fauvel, 1916); *A. fauveli* (Rioja, 1918); *A. grubii* (Marenzeller, 1886); *A. ornata* (Fauvel, 1928); *A. rigida* (Claparède, 1868); *A. sp.*, abbranchiate (see Bellan, 1964).

Distribution. Eastern North Atlantic Ocean and Mediterranean Sea; in shallow depths.

Genus *Kinbergonuphis* Fauchald

Fig. 34a-o

Kinbergonuphis Fauchald, 1982a: 10. Type species: *Onuphis tenuis* Hansen, 1882: 10, by original designation. Gender: feminine.

Material examined. *Onuphis tenuis*—**Brazil:** off Rio de Janeiro—LECTOTYPE and PARALECTOTYPE (RNHL). *Onuphis taeniata*—**Australia:** Queensland: Mackay—HOLOTYPE (AM W.15102) and 7 PARATYPES (AM W.15095-101). *Kinbergonuphis taeniata*—**Australia:** Queensland: Moreton Bay—3 (QM GH570, 572, 574). *K. n.sp.*—**Australia:** Queensland: Moreton Bay near Brisbane—1 (QM GH573); Halifax Bay, N of Townsville—1 (AM W.198983) and others (AM).

Diagnosis. Antennae with short to moderately long ceratophores (3-10 rings); anterior lateral styles longer than their ceratophores; short transition zone of ventral glandular pads with reduced cirri (to setiger 7-9, rarely 11-13) or globular ventral cirri; large median hooks often present.

Definition. Prostomium (Fig. 34a) anteriorly incised or extended. Posterior antennae on median to posterior part of prostomium, with ceratophores with usually 3-7 rings (rarely 8-10 or smooth), and with short to long styles: longest (usually posterior laterals) to setiger 5-25, anterior lateral styles as long as or longer than their ceratophores. Frontal and labial palps oval, with or without median section (Fig. 34b). Nuchal grooves straight, small to large middorsal separation. Tentacular cirri inserted distally on short to moderately long

peristomium, middorsal part of peristomium with anterior fold; ventral lip with median section.

Anterior 5-7 (rarely 3) pairs of parapodia modified, short to slightly prolonged (Fig. 34c,m). Ventral cirri subulate on anterior 2-7 setigers, short transition zone of glandular pads with reduced cirri to setiger 7-9 (rarely 11-13), or globular ventral cirri; dorsal cirri short to moderately long, with or without basal swelling. Branchiae rarely absent, usually present from setiger 6, rarely before or after; rarely single, usually pectinate filaments; branchial stem usually thin (Fig. 34d).

Hooks of modified parapodia usually tridentate (sometimes uni- to tridentate), pseudocompound with hoods (Fig. 34e). Median hooks slightly larger, usually becoming simple and changing to 'large median hooks' (see p. 13) (Fig. 34f-h), present usually in anterior unmodified parapodia, often until origin of subacicular hooks. Pectinate setae (Fig. 34i) from setiger 1 or later; upper limbate setae (Fig. 34j) from setiger 1, lower limbate setae (Fig. 34k) simple; bidentate hooded subacicular hooks (Fig. 34l) usually from setiger 12-20 (rarely later, up to 40).

Jaws with mandibles (Fig. 34n), and maxillae (Fig. 34o) with moderately long Mx III, short Mx V, Mx VI absent. Tubes usually thin, consisting of inner mucous and outer layer of sediment; rarely tough, with parchment-like lining.

Size. Most species are small, less than 10 cm, width less than 2 mm. Width of largest species to 5 mm with parapodia.

Remarks. The genus was recently described by Fauchald (1982a). His diagnosis is accepted in the present definition but a greater emphasis is placed on the large median hooks of anterior setigers. Fauchald stated that pseudocompound hooks were present in the first five setigers of the type species and that large hooks were absent. An examination of the type specimens of *K. tenuis* revealed the presence of large median hooks (Fig. 34a) in setigers 6-8. The large median hooks develop late in ontogeny and are absent in young juveniles (see p. 20). This may account for several small species, listed below, that lack the characteristic hooks.

The following list of recognized species is based on Fauchald (1982a) who gave a key to species. *Onuphis vexillaria* Moore, 1911 is here referred to *Kinbergonuphis* due to the possession of the following characters: antennae with short ceratophores, large number of ventral cirri, numerous branchial filaments, large median hooks and late origin of subacicular hooks. The species marked with an asterisk have long pointed hoods (except *Nothria atlantisa* Hartman, 1965 which lacks hoods) and lack large median hooks. They should probably be referred to the genus *Paradiopatra*: *K. tenuis* (Hansen, 1882); **K. abyssalis* (Fauchald, 1968); ?*K. arctica* (Annenkova, 1946); **K. atlantisa* (Hartman, 1965); *K. cedroensis* (Fauchald, 1968); *K. difficilis* (Fauchald, 1982d); *K. dorsalis* (Ehlers, 1897); *K. fragilis* (Kinberg, 1865); *K. gorgonensis* (Monro, 1933); *K.*

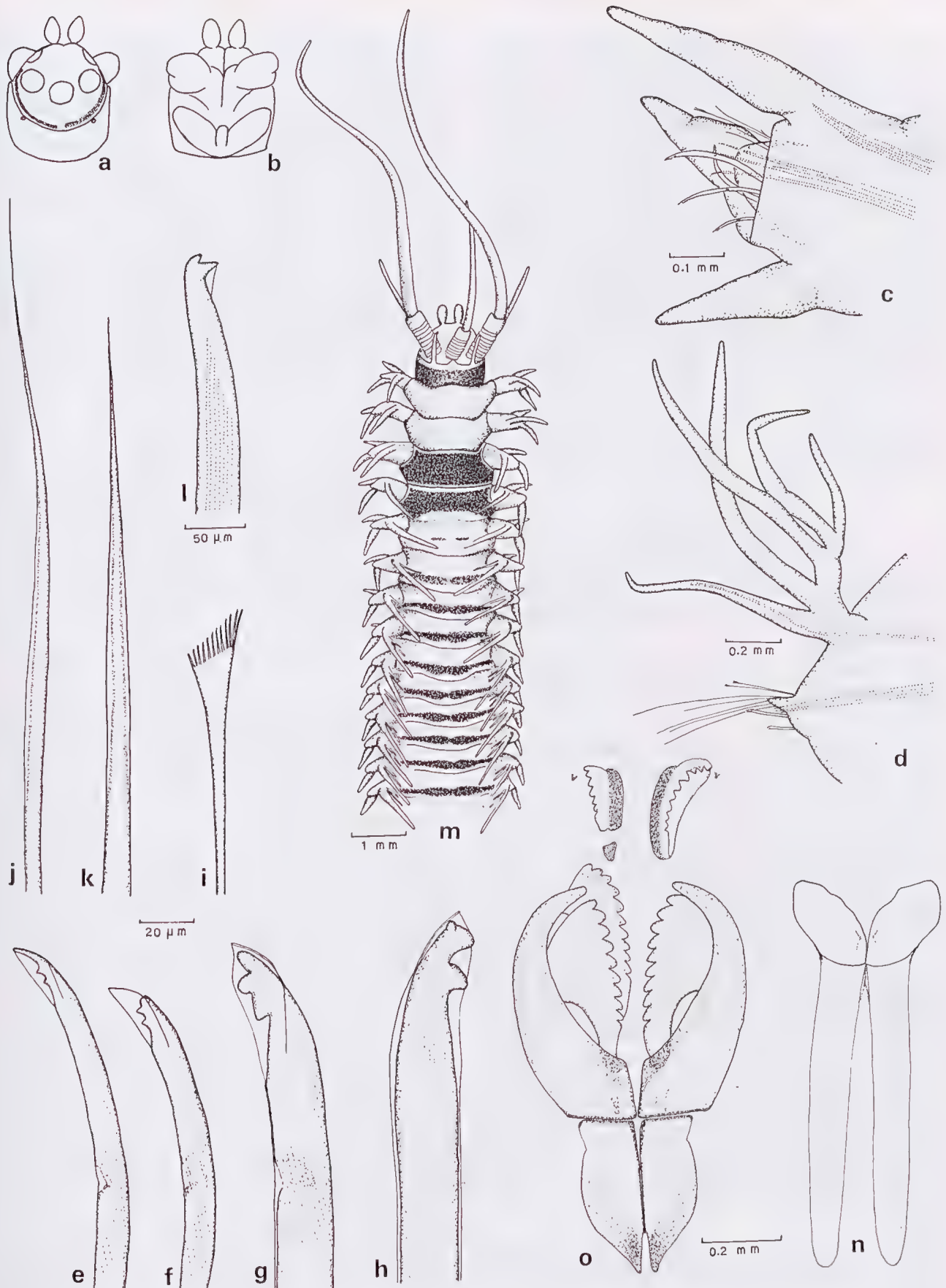


Fig. 34. *Kinbergonuphis tenuis* (d, f, g, lectotype; e, h-m, paralectotype RNHL): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, parapodium 1, anterior view; d, posterior parapodium, posterior view; e, upper pseudocompound hook from setiger 1; f, median pseudocompound hook from setiger 1; g, pseudocompound 'large median hook' from setiger 4; h, simple 'large median hook' from setiger 8; i, pectinate seta from posterior setiger; j, upper limbate seta from setiger 6; k, lower limbate seta from same; l, subacicular hook from posterior setiger. *Kinbergonuphis taeniata* (from Paxton, 1979: figs 43, 54, 55): m, anterior part, dorsal view; n, mandibles; o, maxillae (Mx III to Mx V not in natural position).

heterouncinata (Hartmann-Schröder, 1965) (? juvenile); *K. investigatoris* (Fauvel, 1932); *K. jenneri* (Gardiner, 1976); *K. lineata* (Fauchald, 1980); *K. microcephala* (Hartman, 1944); **K. mixta* (Fauchald & Hancock, 1981); ?*K. multidentata* (Hartmann-Schröder, 1960); *K. nannognathus* (Chamberlin, 1919); *K. notialis* (Monro, 1930); *K. oligobranchiata* (Orensanz, 1974); *K. orensanzi* (Fauchald, 1982d); *K. paradiopatra* (Hartman, 1944); *K. pigmentata* (Fauchald, 1968); *K. proalupus* (Chamberlin, 1919); *K. pseudodibranchiata* (Gallardo, 1968); *K. pulchra* (Fauchald, 1980); *K. pygidialis* (Fauchald, 1968) (? juvenile); *K. rubescens* (Augener, 1906); *K. simoni* (Santos, Day & Rice, 1981); *K. taeniata* (Paxton, 1979); *K. tenuisetis* (McIntosh, 1885); *K. vermillionensis* (Fauchald, 1968); *K. vexillaria* (Moore, 1911); *K. virgata* (Fauchald, 1980); *K. n.sp.*

Distribution. World-wide, in all depths; most species occur in the western Atlantic Ocean, in intertidal depths (see Fauchald, 1982a).

Genus *Mooreonuphis* Fauchald

Fig. 35a-j

Mooreonuphis Fauchald, 1982a: 55. Type species: *Onuphis nebulosa* Moore, 1911: 269, by original designation. Gender: feminine.

Material examined. *Onuphis nebulosa*—U.S.A.: California: Monterey Bay—2 PARATYPES (USNM 17062) and 4 (USNM 17432).

Diagnosis. Anterior hooks bi- to tridentate; lower limbate setae compound (= spinigers).

Definition. Prostomium (Fig. 35a) anteriorly weakly incised or extended. Posterior antennae on median to posterior part of prostomium with ceratophores with up to 5 rings, rarely smooth, with short to long styles: longest (usually posterior laterals) to setiger 3–13, anterior lateral styles longer than their ceratophores. Frontal and labial palps oval, without median section (Fig. 35b). Nuchal grooves straight, small middorsal separation. Tentacular cirri inserted distally on short to moderately long peristomium, middorsal part of peristomium with anterior fold; ventral lip with median section.

Anterior 3–5 (rarely 7) pairs of parapodia modified, not prolonged (Fig. 35c). Ventral cirri subulate on anterior 3–6 setigers (rarely up to 10), short transition zone of globular ventral cirri; dorsal cirri short to moderately long. Branchiae usually present after setiger 17 (rarely from 6 or 7); usually single, rarely pectinate filaments.

Hooks of modified parapodia usually tridentate (rarely bi- and tridentate), pseudocompound with hoods (Fig. 35d–f). Median hooks slightly larger (Fig. 35e), sometimes becoming simple and changing to 'large median hooks' (see p. 31) (Fig. 35g), and present in anterior unmodified parapodia. Pectinate setae from setiger 6–7, upper limbate setae from setiger 1, lower setae compound (= spinigers) (Fig. 35h) until replaced

by bidentate hooded subacicular hooks (Fig. 35i) from setiger 13–29.

Jaws with mandibles, and maxillae (Fig. 35j) with moderately long Mx III, small Mx V, Mx VI absent. Tubes range from thin mucous to tough parchment-like inner layer with outer layer of sediment.

Size. Small; length less than 10 cm, width up to 2.2 mm with parapodia.

Remarks. The following list of recognized species is based on Fauchald (1982a) who gave a key to species. *Nothria exigua* Shisko, 1981 and *Onuphis segmentispadix* Shisko, 1981 possess spinigers and are here referred to *Mooreonuphis*: *M. nebulosa* (Moore, 1911); *M. cirrata* (Hartman, 1944); *M. dangrigae* (Fauchald, 1980); *M. exigua* (Shisko, 1981); *M. guadalupensis* (Fauchald, 1968); *M. intermedia* (Kinberg, 1865); *M. jonesi* Fauchald, 1982c; *M. litoralis* (Monro, 1933); *M. microbranchiata* (Fauchald, 1968); *M. pallidula* (Hartman, 1965); *M. peruana* (Hartman, 1944); *M. segmentispadix* (Shisko, 1981); *M. stigmatis* (Treadwell, 1922); *M. veleronis* (Fauchald, 1980).

Distribution. Eastern Pacific and western Atlantic Oceans: Americas; in intertidal to shelf depths (see Fauchald, 1982a).

Genus *Onuphis* Audouin & Milne Edwards

Figs 3, 6–8, 10

Onuphis Audouin & Milne Edwards, 1833: 225. Type species: *Onuphis eremita* Audouin & Milne Edwards, 1833: 226, by subsequent designation of Malmgren, 1866: 180. Gender: feminine.

Material examined. *Onuphis eremita*—France: Noiremountier, near St. Nazaire—2 (BMNH ZK 1928.4.26.290-1). *O. aucklandensis*—New Zealand: Auckland—several (UC). *O. holobranchiata*—Australia: Queensland—many (AM); Victoria: Phillip Island—1 (AM W.3584) and others (NMV); Western Australia: Cockburn Sound—1 (WAM 23-74) and others. *O. n.sp.*, abranchiate—Australia: New South Wales: Botany Bay near Sydney—10' (AM W.13117) and others (AM).

Diagnosis. Antennae with moderately long to long ceratophores (10–25 rings) and short to moderately long styles; anterior lateral styles shorter than their ceratophores; branchiae usually from setiger 1.

Definition. Prostomium (Fig. 3a,b) often anteriorly extended. Posterior antennae on median to posterior part of prostomium, with ceratophores usually with 10–25 rings (rarely less than 10), with short to moderately long (rarely long) styles: longest (posterior laterals) to setiger 5–12 (rarely to 25), anterior lateral styles shorter than their ceratophores. Frontal and labial palps oval, with or without median section (Fig. 3c). Nuchal grooves straight, small to wide middorsal separation. Tentacular cirri inserted distally on moderately long peristomium. Middorsal part of peristomium with distinct anterior fold; ventral lip with median section.

Anterior 3–4 (rarely 2 or 5) pairs of parapodia modified, not prolonged (Figs 3a, 6a). Ventral cirri subulate on anterior 4–6 setigers, short transition zone of globular ventral cirri; dorsal cirri moderately long, with basal swelling. Interramal papillae (Fig. 6b) on setigers 4–10 in type species. Branchiae rarely absent, usually present from setiger 1, rarely 3–6; usually thin stem (Fig. 7), single or pectinate filaments (maximum 8).

Hooks of modified parapodia usually tridentate (rarely only bidentate, sometimes bi- and tridentate), pseudocompound with hoods (Fig. 8d,e); median hooks usually slightly larger (Fig. 8d) but not becoming simple or remaining into unmodified parapodia. Pectinate setae (Fig. 8c) and upper limbate setae (Fig. 8a) from setiger

1 or later; lower limbate setae (Fig. 8b) simple; bidentate hooded subacicular hooks (Fig. 8f) usually from setiger 10–12 (rarely 9–18).

Jaws with mandibles (Fig. 9a), and maxillae (Fig. 9b) with moderately long Mx III, small Mx V, Mx VI absent. Tubes usually thin, consisting of inner mucous and outer layer of sediment; rarely tough with parchment-like lining.

Size. Most species are small, width less than 3 mm. Length of largest species is up to 30 cm (more than 200 setigers) width up to 4 mm.

Remarks. Audouin & Milne Edwards (1833) did not designate a type species for *Onuphis*. The description

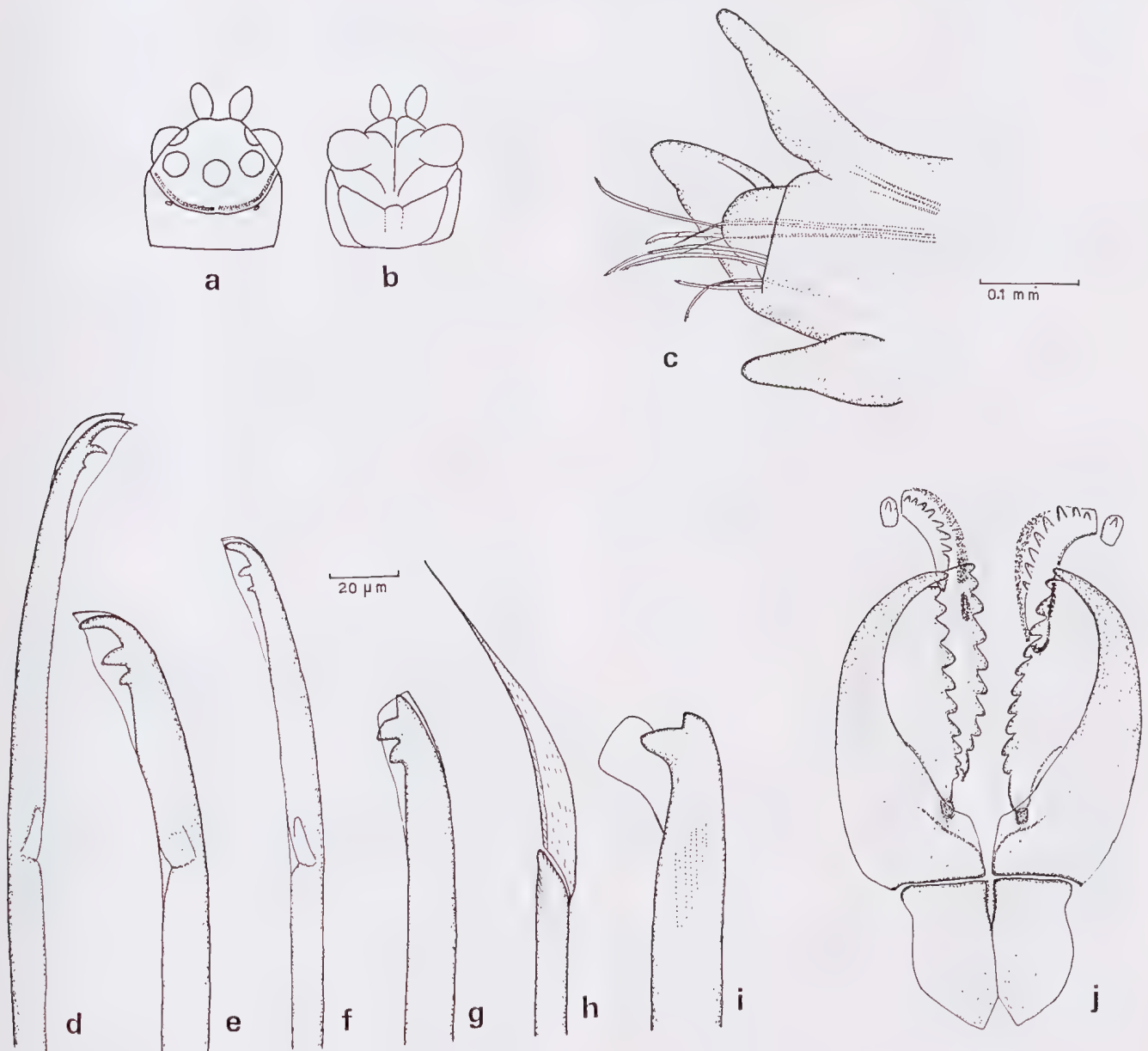


Fig. 35. *Mooreonuphis nebulosa* (a–g, i–j, USNM 17432; h, paratype USNM 17062): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, parapodium 1, anterior view; d, upper pseudocompound hook and peristomium, dorsal view; e, same, ventral view; f, lower pseudocompound hook from same; g, simple 'large' hook from setiger 1; h, compound lower limbate seta from setiger 12; i, subacicular hook from posterior setiger; j, maxillae.

of the genus was followed by that of *Onuphis eremita* with a note that *Nereis tubicola* Müller also belonged to the genus *Onuphis*. Therefore, *O. eremita* cannot be considered as type species by monotypy as has been stated by some authors. Milne Edwards (1838: 564) gave a short description of the genus and listed only one species, *Onuphis eremita*. This reference was taken as a type designation by Malmgren (1866) and stated as such. Thus, the first author to unequivocally state the type species for the genus was Malmgren and his subsequent designation is herein accepted.

The genus was recently revised by Fauchald (1982a), whose diagnosis is largely accepted in the present definition. However, the discovery of an abbranchiate new species (Paxton, in preparation), fitting the definition of the genus *Onuphis* in all other criteria, requires the emendation of the genus to include abbranchiate species.

The following list of recognized species is based on Fauchald (1982a) who gave a key to species: *O. eremita* Audouin & Milne Edwards, 1833; *O. eremita oculata* Hartman, 1951 (? juvenile *O. eremita*); *O. eremita parva* Berkeley & Berkeley, 1941; *O. aucklandensis* Augener, 1924; *O. branchiata* Treadwell, 1931; *O. chinensis* Uschakov & Wu, 1962; *O. declivorum* Fauchald, 1982c; *O. dibranchiata* Willey, 1905; *O. elegans* (Johnson, 1901); *O. falesia* Castelli, 1982; *O. farallonensis* Hobson, 1971; *O. geophiliformis* (Moore, 1903) (? juvenile); *O. heterodentata* Fauchald, 1982c; *O. holobranchiata* Marenzeller, 1879; *O. iridescens* (Johnson, 1901); *O. lithobiformis* Fauchald, 1982c; *O. mexicana* (Fauchald, 1968); *O. multiannulata* Shisko, 1981; *O. opalina* (Verrill, 1873); *O. pallida* (Moore, 1911); *O. rullieriana* (Amoureux, 1977); *O. shirikishinaiensis* (Imajima, 1960); *O. similis* (Fauchald, 1968); *O. texana* Fauchald, 1982c (? juvenile); *O. vibex* (Fauchald, 1972); *O. n.sp.* (abbranchiate.)

Distribution. World-wide, in all depths; most species occur in the western Pacific Ocean, in shelf depths (see Fauchald, 1982a).

Genus *Heptaceras* Ehlers

Fig. 36a-j

Heptaceras Ehlers, 1868: 284. Type species: *Diopatra phyllocirra* Schmarda, 1861: 133, by monotypy. Gender: neuter.

Tradopia Baird, 1870: 355. Type-species: *Tradopia maculata* Baird, 1870: 355, by monotypy.

Material examined. *Diopatra phyllocirra*—Sri Lanka: south west, Bentota Beach—NEOTYPE designated herein (BMNH ZK 1953.11.10.8). *Heptaceras phyllocirrum*—Sri Lanka: south west, Bentota Beach—1 (BMNH ZK 1953.11.10.1-7); Arabia: south coast—3 (BMNH ZK 1937.9.2.341-2). *Tradopia maculata*—India: Madras—2 SYNTYPES (BMNH ZK 1868.5.27.1). *Onuphis quinquedens*—South Africa: Natal: Umpanganzi—HOLOTYPE (BMNH ZK 1961.16.34).

Diagnosis. Antennae with long to very long ceratophores (20–60 rings); peristomium with deep middorsal notch.

Definition. Prostomium (Fig. 36a) with frontal extension forming palpophores for frontal palps. Posterior lateral antennae on posterior part of prostomium, median antenna in more anterior position; ceratophores very wide (almost covering dorsal part of prostomium) and long (20–60 rings), styles short to moderately long; longest (posterior laterals) to setiger 3–10; anterior lateral styles shorter than their ceratophores. Frontal palps oval; labial palps rectangular, with small median section (Fig. 36b). Moderately long peristomium with deep middorsal notch; ventral lip with median section. Nuchal grooves following edge of peristomium including notch, separated in midline by raised ridge between base of notch and base of median antenna. Tentacular cirri inserted distally on peristomium on each side of notch.

Anterior 3 pairs of parapodia modified, slightly prolonged (Fig. 36c). Ventral cirri subulate, present on anterior 5 setigers, short transition zone of globular ventral cirri; dorsal cirri moderately long, with basal swelling, small basal process present (Fig. 36d) or absent. Small interrampal papilla from setiger 6–10 in type species. Branchiae from setiger 1, with thick stem and pectinate filaments (maximum of 12).

Hooks of modified parapodia bi- to tridentate, pseudocompound with hoods (Fig. 36e,f,i,j); median hooks slightly larger but not becoming simple or being present in anterior unmodified parapodia. Pectinate setae from setiger 6–8; upper limbate setae from setiger 1, lower limbate setae simple; bidentate hooded subacicular hooks (Fig. 36g) from setiger 9–10.

Jaws with mandibles, and maxillae (Fig. 36h) with moderately long Mx III, small Mx V, Mx VI absent. Worms make mucous-lined vertical burrows (Day, 1967), i.e. temporary tubes.

Size. Moderately large; width to 4 mm; length to 20 cm (500 setigers).

Remarks. The genus *Heptaceras* was erected by Ehlers (1868) for *Diopatra phyllocirra*, described by Schmarda (1861) from the east and south coasts of Sri Lanka. It has not been reported since its original description and has been considered a probably aberrant form by Kucheruk (1978).

Ehlers defined the genus as having long, filiform frontal palps, resembling the antennae, instead of the short frontal palps present in *Diopatra*. However, Schmarda never stated that the frontal palps of *D. phyllocirra* were as long as the antennae, on the contrary, he compared their length to that of the tentacular cirri which he described as small, 'hardly larger than those of the forehead'.

He described the head as small, with two eyes at the base of the median antenna, and next to them the tentacular cirri. He stated that branchiae were present from setiger 1 as a single filament, becoming spiralled later. Spiralled branchiae are known to occur only in *Diopatra* and *Epidiopatra*, where they are spiralled from their origin on setiger 4–5. The filaments in Schmarda's illustration (fig. f) appear more pectinately branched

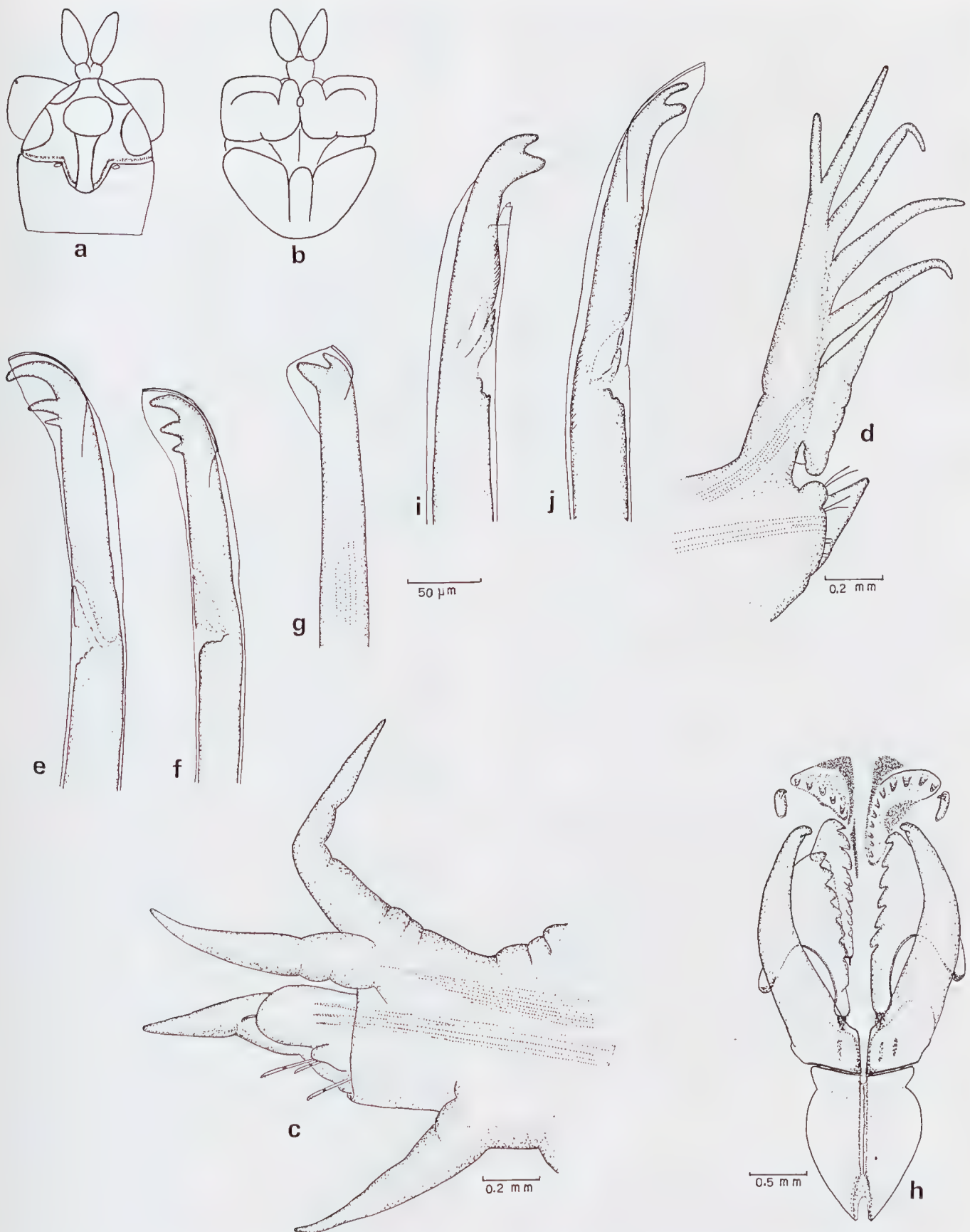


Fig. 36. *Heptaceras phyllocirrum* (BMNH ZK 1953.11.10.1-8): **a**, stylized diagram of prostomium and peristomium, dorsal view; **b**, same, ventral view; **c**, parapodium 1, anterior view; **d**, parapodium 17, anterior view; **e**, median tridentate pseudocompound hook from setiger 1; **f**, lower tridentate pseudocompound hook from same; **g**, subacicular hook from setiger 98; **h**, maxillae. *Heptaceras quinquedens* (holotype BMNH ZK 1961.16.34): **i**, median bidentate pseudocompound hook from setiger 2; **j**, lower bidentate pseudocompound hook from same.

than spiralled. Another characteristic of the species was the leaf-like, uneven heart-shaped dorsal cirrus (Schmarda, 1861: fig. f).

Baird (1870) described the genus *Tradopia* for his new species *T. maculata*. The genus was considered invalid and *T. maculata* referred to *Onuphis* (Hartman, 1959; Fauchald, 1977). The species had not been reported since its original description. This may be attributed to Baird's insufficient description which was not accompanied by any illustrations. Examination of the type material shows that *T. maculata* has a small prostomium, almost completely covered by the large ceratophores of the antennae, has dorsal cirri with basal processes (giving a heart-shaped appearance), has branchiae from setiger 1, which become pectinately branched from setiger 10, and its subacicular hooks are of the same shape as those illustrated by Schmarda (1861: fig. c) for *D. phyllocirra*. Although *T. maculata* lacks eyes, the depressions next to the median ridge between the peristomium and the base of the median antenna flanked by the tentacular cirri could have been interpreted as eyes. It appears certain that *T. maculata* is a junior synonym of *D. phyllocirra*.

Onuphis basipicta Willey, 1905: 275, from southwest Sri Lanka, is also referred to the latter. Although the type material is not available (Fauchald, 1982a), its identity appears clear from the description. Furthermore, specimens from Bentota Beach, S.W. Sri Lanka, have been identified as the same species in the present study, marking it as a common species on the Sri Lankan coasts. However, it also occurs on the South Arabian coast [it had been misidentified by Monro (1937: 292) as *O. eremita*] and near Madras, so that it is much more common and widespread than was previously suspected.

Since the types of *D. phyllocirra* are lost [Kritscher (NMW), personal communication] I am here designating the complete specimen from Bentota Beach, south west Sri Lanka (BMNH ZK 1953.11.10.8), neotype of *Diopatra phyllocirra* Schmarda, 1861.

The genus *Heptaceras* is redefined, placing emphasis on its notched peristomium and very long ceratophores, and is considered a well characterized, valid genus.

The following species are recognized: *H. phyllocirrum* (Schmarda, 1861); *H. fukianensis* (Uschakov & Wu, 1962); *H. quinquedens* (Day, 1951).

Distribution. Indo-Pacific Oceans: South Africa, Arabia, Sri Lanka, India, Taiwan Strait; intertidal to 22 m.

Key to Species of *Heptaceras*

1. Ceratophores of antennae with brown pigment spots; all pseudocompound hooks tridentate (Fig. 36e,f). . . . *H. phyllocirrum*
- Ceratophores of antennae without pigment; pseudocompound hooks bi-, or bi- and tridentate. 2

2. All pseudocompound hooks bidentate (Fig. 36i,j); bifid branchial filaments from setiger 9. *H. quinquedens*
- Pseudocompound hooks bi- and tridentate; bifid branchial filaments from setiger 47. *H. fukianensis*

PHYLOGENETIC RELATIONSHIPS

The phylogenetic relationships within the family Onuphidae are analyzed following the principles of Hennig (1966), where only the derived or apomorphic states of characters are utilized. The character states are determined by outgroup comparison, fossil evidence, and observed ontogenetic changes.

The most useful method is by outgroup comparison. The closest relative or sister group of the Onuphidae is the family Eunicidae. The synapomorphies they share are a similar jaw apparatus, parapodial structures and the possession of antennae. The members of the Onuphidae compose the 'ingroup', while members of the Eunicidae form the 'outgroup'. Since the Onuphidae is more specialized in having distinct frontal palps and antennae with well developed ceratophores, and thus represents the most derived family of the order Eunicida, the comparisons are limited to 'below' (more primitive than) their level of structural organization. The outgroup comparison is based on the examination of representative species of eunicids (see 'Materials and Methods'), and information from the literature.

The Eunicida is the order of polychaetes best represented in the fossil record. Although these are generally limited to isolated maxillae (scolecodonts) and mandibles, complete jaw apparatuses (Kielan-Jaworowska, 1966) and a few complete animals with impressions of parapodial structures and setae (Kozur, 1971; Thompson & Johnson, 1977) are known.

Ontogenetic character transformations can be used to determine adult character states. In a transformation from a more general to a specialized character, the former can be regarded as ancestral and the latter as derived (Nelson, 1978). This method confirms some of the decisions based on the other two criteria utilized.

The analysis is based on 46 morphological and ecological characters which are listed and discussed below. While examination is limited to type species and other selected species, information from the literature is also taken into account. However, some characters used in this analysis (e.g. prostomial features, ultrastructure of setae) have not been described before, so that their possible irregular distribution within genera could provide a source of error. For a number of characters (character 31–33) the derived state could not be determined with certainty. However, these characters have been included, since they are considered important in the definition of taxa.

Some characters have been noted to occur infrequently and are considered retained plesiomorphies with widely spread derived states (34–43). The

determination of the state of the last three characters (44–46) is rather speculative. It is not based on the eunicids as an outgroup, but on the assumption that the state that occurs in both subfamilies is plesiomorphic, unless it has arisen independently.

Discussion of Characters and Their States

The following notation is used: (0) = plesiomorphic state, (1) = apomorphic state, C = by outgroup comparison, F = fossil evidence, J = ontogenetic changes. The distribution of the character states among the genera is tabularized (Table 4).

1. Frontal palps absent (0), present (1); C, J. Some species of *Eunice* (e.g. *E. aphroditois*) have labial palps which are medially incompletely subdivided, but do not represent distinct frontal palps which are absent throughout the family Eunicidae. Frontal palps are absent in young onuphid juveniles and are often the last prostomial structures to develop (see p. 19).

2. Ceratophores absent, or very short, one-ringed (0), present, longer, sometimes smooth, usually with 2 or more rings (1); C, J. The antennae of eunicids have usually a small, more or less defined proximal division which might be considered as a primitive, one-ringed ceratophore. However, it never develops into a 2-ringed or longer structure. Ceratophores are poorly formed in otherwise well developed juvenile onuphids (see p. 19), demonstrating their derived character state.

3. Lower limbate setae present after origin of subacicular hooks (0), absent (1); C. The lower bundle of setae in eunicids consists of compound falcigers and/or limbate setae (= spinigers). These lower setae are present throughout the median and posterior region in eunicids and in the onuphid subfamily Hyalinoeciinae. Their loss in the median and posterior region of the Onuphinae is seen as a specialization to their tubicolous mode of living.

4. Notoetae present (0), absent (1); C, F. Reduced notoetae are present or absent in the Eunicidae. A well preserved fossil eunicid from the Upper Carboniferous, described as a new genus, *Esconites* Thompson & Johnson, 1977, was characterized by the possession of well developed noto- and neuropodia. However, it is clear from the photograph of the setal impressions (Thompson & Johnson, 1977: fig. 8) that the setae referred to as notoacacula are neuroacacula, and the setae referred to as neuroacacula are subacicular hooks. The notoetae were either absent or left no impression, and the species is uni- or subbiramous like other Eunicida. Since the polychaete parapodium is typically biramous, the presence of notoetae in the Onuphinae is considered as the ancestral condition.

5. Subacicular hooks in ventral position (0), median position (1); C, F. In the former condition, the hooks originate at or slightly above the acicula and emerge lower, thus forming an acute angle (see p. 14). This condition is found in all Recent eunicids, and also in fossil eunicids (see above). The subacicular hooks of the fossil genus *Eunicites* Ehlers, 1868 were referred to as small acicula, running at an acute angle to the large

acicula (Kozur, 1971). Anterior permanent subacicular hooks of very young *Diopatra* juveniles are in a median position parallel to the aciculum (see p. 20). The same position in adults of the Hyalinoeciinae is considered as a neotenic condition. The character is considered derived in agreement with Fauchald (1982a), who referred to them as intrafascicular hooks (see p. 13).

6. Hooks without rows of spines (0), with 2 rows of spines (1); C. Small, irregularly distributed spines are present on the shafts of eunicid and onuphid hooks (see p. 13). However, in some genera of onuphids these spines are lengthened and oriented into two lengthwise rows, which is considered a derived condition.

7. Branchiae present throughout (0), limited to anterior region (1); C. Although branchiae are present throughout in all eunicids examined, a number of species are reported in the literature in which the branchiae are limited to the anterior region. The latter condition is considered derived and presumed to have arisen independently in the two families.

8. Lateral projections on ceratophores absent (0), present (1); C. Eunicids lack well developed ceratophores and lateral projections. In the Onuphidae the projections are limited to some species of *Diopatra*, *Epidiopatra*, and *Paradiopatra*. They are present in small species and may represent a neotenic feature, which is considered apomorphic.

9. Rings on ceratophores 10 or less (0), more than 10 (1); C, J. As stated above (character 2), while one-ringed ceratophores may be present in Eunicidae, well developed ones occur only in the Onuphidae. Most genera have short ceratophores with less than 10 rings, which is interpreted to be the ancestral condition, while long ceratophores with many rings (up to 25–60 in some species of *Onuphis* and *Heptaceras*) are interpreted to be the derived condition in agreement with Fauchald (1982a). This is not a unique development but has arisen independently also in *Hirsutonuphis*, *Diopatra* and *Epidiopatra*.

10. Branchial filaments simple or branched (0), spiralling around a central trunk (1); C. Spiralled branchial filaments are a unique development in the Eunicida, restricted to *Diopatra* and *Epidiopatra*, and is a synapomorphy.

11. Tentacular cirri present (0), absent (1); C, J. Tentacular cirri are present in *Eunice* (Eunicidae) and generally in onuphids. In some species they develop relatively late in ontogeny (see p. 19), and their complete absence is considered a derived neotenic character that has evolved independently several times in the Onuphidae.

12. Setal sacs of modified parapodia to setiger 1 (0), to setiger 5 or beyond (1); C. Setal sacs in eunicids and usually onuphids are limited to their respective setiger. However, in genera of the *Rhamphobrachium* complex the setal sacs lie in the body cavity to setiger 5 or later (up to setiger 70), and slide anteriorly when protruded. The structure and function of this setal arrangement is so specialized that it is thought to have evolved only once, and is considered apomorphic.

Table 4. Data used in computing the Wagner tree; the characters and their states are defined in the text.
0.0 = plesiomorphic or unknown state; 0.5 = apomorphic state present in some species of the genus only;
1.0 = apomorphic state. The data was read into the program in the order shown.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Genus																							
<i>Ancestor</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Nothria</i>	1.0	1.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0
<i>Anchinothria</i>	1.0	1.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0
<i>Hyalinoecia</i>	1.0	1.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Leptoecia</i>	0.0	1.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Neonuphis</i>	0.0	1.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Hyalospinifera</i>	1.0	1.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Notonuphis</i>	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Paradiopatra</i>	1.0	1.0	1.0	0.0	0.0	0.5	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Diopatra</i>	1.0	1.0	1.0	0.0	0.0	0.5	1.0	0.5	0.5	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Epidiopatra</i>	1.0	1.0	1.0	0.0	0.0	0.5	1.0	0.5	0.5	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Brevibrachium</i>	1.0	1.0	1.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Longibrachium</i>	1.0	1.0	1.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Rhamphobranchium</i>	1.0	1.0	1.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Americonuphis</i>	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Australonuphis</i>	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0
<i>Hartmanonuphis</i>	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Hirsutonuphis</i>	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0
<i>Aponuphis</i>	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Kinbergonuphis</i>	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0
<i>Mooreonuphis</i>	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0
<i>Onuphis</i>	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.5	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Heptaceras</i>	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0

Character	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
Genus																							
<i>Ancestor</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Nothria</i>	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.5	1.0	1.0	0.5	1.0	1.0	0.5	1.0	1.0	1.0	0.0	0.0	0.0
<i>Anchinothria</i>	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.5	1.0	1.0	0.5	1.0	1.0	1.0	1.0	0.5	1.0	0.5	0.0	0.0
<i>Hyalinoecia</i>	0.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	1.0	1.0	0.5	1.0	0.5	0.5	0.5	1.0	0.0	0.0	0.0	0.0
<i>Leptoecia</i>	0.0	0.0	1.0	0.0	1.0	1.0	1.0	0.0	1.0	1.0	0.0	1.0	1.0	0.5	1.0	0.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
<i>Neonuphis</i>	0.0	0.0	1.0	0.0	1.0	1.0	0.0	0.0	1.0	1.0	0.0	1.0	1.0	0.0	1.0	0.5	0.5	0.5	1.0	0.0	0.0	0.0	0.0
<i>Hyalospinifera</i>	0.0	0.0	1.0	0.0	1.0	1.0	1.0	0.0	1.0	1.0	0.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
<i>Notonuphis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0
<i>Paradiopatra</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.5	0.5	1.0	0.5	1.0	0.5	1.0	1.0	1.0	0.0	1.0	0.5	1.0
<i>Diopatra</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.5	1.0	0.5	1.0	0.5	0.5	1.0	1.0	0.0	1.0	1.0	1.0
<i>Epidiopatra</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.5	1.0	0.5	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0
<i>Brevibrachium</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.5	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.5	0.5	0.5	1.0
<i>Longibrachium</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	1.0	1.0	1.0	0.5	0.0	1.0	0.5	0.0	1.0	1.0	1.0
<i>Rhamphobranchium</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.5	1.0	1.0	1.0	0.5	1.0	0.0	0.5	1.0	0.0	0.5	0.5	1.0
<i>Americonuphis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.5	1.0	0.0	1.0	1.0	0.0	1.0	0.0	0.0	1.0	1.0	1.0
<i>Australonuphis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	0.0	1.0	0.5	0.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0
<i>Hartmanonuphis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0
<i>Hirsutonuphis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	0.5	0.5	1.0	0.5	1.0	1.0	1.0	0.0	1.0	1.0	1.0
<i>Aponuphis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.5	1.0	1.0	1.0	0.0	0.0	1.0	1.0
<i>Kinbergonuphis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.5	1.0	1.0	1.0	0.5	1.0	1.0	1.0	0.0	1.0	1.0	1.0
<i>Mooreonuphis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.5	1.0	1.0	0.0	0.5	1.0	1.0	1.0	0.0	0.5	0.5	1.0
<i>Onuphis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.5	1.0	0.5	1.0	1.0	1.0	1.0	0.5	0.0	0.5	1.0	1.0
<i>Heptaceras</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	1.0	1.0	0.5	1.0	1.0	1.0	1.0	0.0	0.0	1.0	1.0	1.0

13. Setal sacs of modified parapodia to setiger 1–5 (0); to setiger 20 or beyond (1); C. The very long setal sacs of *Rhamphobrachium* and *Longibrachium* are here considered an extreme specialization of the two genera.

14. Hooks with immoveable spines (0), with moveable spines (1). Rows of spines are absent in eunicid hooks, which can therefore not be used as the outgroup for this character. The immoveable spines (see p. 13) present in a number of genera are of a simpler type than the highly specialized moveable spines which are only found in *Rhamphobrachium*. Although it cannot be proven at the present time, the former are considered ancestral and the latter derived.

15. Modified parapodia positioned more ventrally than unmodified ones and directed ventrally to anteroventrally (0), anterolaterally to -dorsally (1), C. All eunicid parapodia are similar but the anterior ones are positioned more ventrally and are in contact with the substratum, allowing a crawling method of locomotion. This ventral position of the parapodia has been maintained in some onuphid genera (e.g. *Notonuphis*, *Paradiopatra*). Members of other genera retained the ventral position but developed prolonged anterior parapodia [e.g. *Diopatra* (Fig. 1a), *Rhamphobrachium*, *Nothria*] which became anteroventrally directed. Both types are considered ancestral, while the anterolateral to -dorsal position and direction of *Australonuphis* (Fig. 1b) and related genera is considered derived.

16. Mx V large or Mx VI present (0), Mx V small and Mx VI absent (1), C. Maxilla VI is present in some but not all species of *Eunice*. Mx V is large in all eunicid species examined, and has also been illustrated as such in the literature. The small Mx V of the *Onuphis* group is interpreted here as a derived character.

17. Anterior peristomial fold present (0), absent (1); C. A distinct dorsal anterior fold is present in all eunicids and most onuphids. In *Australonuphis* and related genera the peristomium lacks this fold, appearing to extend along the curved nuchal grooves toward the median antenna. This condition is considered as an adaptation to the beach habitat and thus an apomorphic condition.

18. Maxillary carriers uniformly sclerotized (0), median and lateral strong sclerotization (1); C. The maxillary carriers of eunicids and all other genera of onuphids are uniformly sclerotized; the unique sclerotization found in *Hirsutonuphis* is considered an autapomorphy.

19. Subacicular hooks distally bidentate (0), distally entire (1); C. Subacicular hooks are distally bidentate in all but one species of eunicids examined, as they are in most reported species of the family and in all onuphid genera except *Australonuphis*. The distally entire hooks are considered an apomorphy that evolved independently in some species of *Eunice* and *Australonuphis*.

20. Peristomium complete (0), with deep anterior middorsal notch (1); C. The peristomium of eunicids and all other genera of onuphids is anteriorly complete,

and the deep middorsal notch found in *Heptaceras* is considered an autapomorphy.

21. Large median hooks absent (0), present (1); C. J. Large median hooks (see p. 13) are not present in the Eunicidae. Their presence in two genera of Onuphidae is here considered derived, as it was by Fauchald (1982a). The late development of large median hooks (see p. 20) also supports their derived state.

22. Pectinate setae flat (0), scoop-shaped (1); C. Pectinate setae are flat or slightly rolled up in all eunicids and onuphids except *Nothria* and *Anchinotria*. In these two genera the lateral distal parts are flared towards each other forming an 'open scoop' (see p. 12), which is considered an apomorphic character in agreement with Fauchald (1982a).

23. Maxilla III distally shorter than left Mx II (0), longer (1); C. In the species of Eunicidae examined, and probably all species of the family, the Mx II is distally shorter than Mx III as it is in all genera of Onuphidae except *Nothria* and *Anchinotria*. This condition is considered plesiomorphic, and the distally longer Mx II a synapomorphy of the latter two genera.

24. Tubes absent, of parchment-like material, or consisting of inner secreted and outer layer of foreign particles, round in transverse section (0), flat tubes with outer layer of foreign particles attached with the flat or concave side to the lining (1); C. Most eunicids have no tubes while some species construct completely organic, parchment-like tubes. While the *Nothria* tubes consist of a secreted inner layer and an outer layer of foreign particles like most onuphid tubes, they are characteristic in their orientation and attachment of the particles and are here interpreted as autapomorphic.

25. Branchial filaments simple or pectinate (0), dichotomously branched (1); C. Dichotomously branched branchial filaments are not found in any eunicids or other onuphids, and are considered autapomorphic in species of *Anchinotria*.

26. Tubes (see plesiomorphic state of character 24) (0), consisting of a clear material composed of onuphic acid and mucoprotein (1); C. Completely organic tubes of an opaque parchment-like material are secreted by eunicids and two species of *Epidiopatra* (Onuphinae), and are considered plesiomorphic, while the clear tubes of the Hyalinoeciinae are considered apomorphic.

27. Tubes without internal valves (0), with internal valves (1); C. The presence of internal valves in *Hyalinoecia* tubes is unique in the order Eunicida, and thus an autapomorphic character.

28. Maxillary cavity openings short to moderately elongated (0), very elongated (1); C, F. The maxillary cavity openings are short to moderately long in the species of Eunicidae examined and in literature reports of extant and extinct members of the family. The maxillae I to III of *Neonuphis* and *Leptoecia* have extremely large cavity openings, a condition assumed to occur also in *Hyalospiniifera*, and is considered derived.

29. Maxillae V present (0), absent (1); C, F. Maxillae V are present in all eunicids examined, presumably in

all Recent and fossil species. Their absence in *Neonuphis*, *Leptoecia* and presumably *Hyalospinifera* is considered a secondary loss and thus derived.

30. Tube without secreted lateral rods (0), with 1 or 2 secreted lateral rods (1); C. Tubes with secreted lateral rods are constructed only by species of *Leptoecia* and *Hyalospinifera* and thus represent a derived character.

31. Oocytes with a single cluster of nurse cells (?0), two strings of nurse cells (?1). Within the order Eunicida, nurse cells are present only in the Dorvilleidae (one cell per oocyte) and Onuphidae. Strings of nurse cells have not been reported for any other group and may represent an autapomorphy of the Onuphinae.

32. Pygidium with four anal cirri (?0), two anal cirri (?1). Anal cirri number two or four in the Eunicidae and no deduction as to the ancestral state can be made based on outgroup comparison. However, it is likely that the ancestral condition was four cirri and became reduced to two in each family independently.

33. Primary envelope of mature oocytes smooth (?0), densely pitted (?1). The more complex surface of the primary envelope may represent the derived condition.

34. Tentacular cirri inserted on second aetigerous segment to subdistally on peristomium (0), distally on peristomium (1); C. Tentacular cirri, when present in the Eunicidae, are inserted far from the anterior margin of the peristomium. In *Americonuphis* the tentacular cirri are inserted in the middle of the peristomium, and in some other genera subdistally. This is considered ancestral, and the distal insertion found in most onuphids is considered derived.

35. Four or more pairs of modified parapodia (bearing hooks) (0), 1–3 pairs (1); C, J. Fauchald considered three to five pairs of parapodia with pseudocompound hooks as plesiomorphic and '(a) two or less' or '(b) more than 5' as apomorphic. In eunicids, all setigers have compound spinigers and/or falcigers. The restriction of hooks to the anterior parapodia and the fusion of the fracture is a specialization of onuphids. I consider it a gradual process with a large number of modified parapodia the ancestral, and a small number the derived condition. Several genera in the Onuphinae retain the plesiomorphic condition. Since the parapodia that have retained hooks usually also bear subulate ventral cirri, the same states are accepted for this character. Agreement between the two characters has been defined as the plesiomorphic, and its absence as the apomorphic condition by Fauchald. As discussed above (see p. 10) the number of setigers with hooks usually agrees with the number of setigers with ventral cirri, while the absence of agreement is usually due to the fact that the first glandular pads also carry reduced cirri (see character 36). Juveniles sometimes bear transitional falcigers in early unmodified parapodia that later disappear (see p. 20). They are considered relicts of the ancestral state, where a greater number of parapodia bore hooks.

36. Long transition zone between subulate ventral cirri and glandular pads (0), short transition zone (1); C. Glandular pads with reduced cirri is the ancestral

condition found in eunicids. In some genera of onuphids this condition is present as a transition zone between ventral cirri and glandular pads. The long transition zone of reduced cirri is considered ancestral, and the short transition zone of either reduced subulate or globular cirri is considered derived.

37. Anterior hooks distally only bidentate (0), tridentate or otherwise (1); C. The ancestral pseudocompound to compound hooks are thought to have been distally bidentate. Fauchald (1982a) took the tridentate condition as primitive, and either unidentate or bidentate alone, or unidentate or bidentate together with tridentate as the apomorphic condition. The hooks of eunicids are bidentate as they are also in some genera of onuphids. Tridentate hooks are absent in the Hyalinoeciinae but common in the Onuphinae, particularly in conjunction with bidentate hooks. The bidentate condition is here taken as the ancestral condition; uni- and tridentate hooks probably evolved independently several times.

38. Compound limbate setae (= spinigers) present (0), absent (1); C. Fauchald (1982a) considered the presence of spinigers in *Mooreonuphis* as an apomorphy. Spinigers are found in a number of eunicids and their presence in onuphids is here considered a retained plesiomorphic character.

39. Late origin of subacicular hooks (after setiger 20) (0), early origin (setiger 8–19) (1); C, J. The origin of subacicular hooks in the eunicids examined ranged from 20–79, and occurs after setiger 20 in most species. The hooks start on setiger 6–8 in small juveniles (see p. 20) and subsequently become displaced more posteriorly. The early origin found in adult onuphids is interpreted as a derived neotenic feature that has arisen many times.

40. Subacicular hooks start as one per parapodium (0), two per parapodium (1), C. In the eunicids examined, subacicular hooks start as one per parapodium. This condition is found in members of the *Diopatra* group and some Hyalinoeciinae, and is considered ancestral, while the common pattern of two hooks per parapodium from their first appearance, as in most onuphids, is considered derived.

41. Three or more subacicular hooks in some parapodia (0), always two (1); C. In some eunicids the subacicular hooks increase to 3–5 per parapodium, a feature that occurs rarely in members of both onuphid subfamilies, and is interpreted as plesiomorphic.

42. Maxilla II wide with laterally protruding ramus (0), narrower ramus not protruding (1); C, F. The wide Mx II with usually laterally protruding ramus is found in Recent and fossil eunicids (see Kielan-Jaworowska, 1966) and considered ancestral, while the narrower Mx II is considered derived. The state is unknown for *Hyalospinifera* and assumed derived as in related genera.

43. Adults consisting of more than 100 segments (0), short-bodied, less than 100 segments (1), C, F. Extant and extinct eunicids consist of a great number of segments (200–1000) which is considered plesiomorphic, while the shortened bodies of some onuphids are

considered apomorphic, in agreement with Fauchald (1982a).

44. Branchial filaments single, strap-like (0), branched or spiralled (1). Fauchald (1982a) considered two or more filaments plesiomorphic and single ones apomorphic. This is a logical assumption, considering the widespread occurrence of pectinate branchiae in eunicids. However, the absence of pectinate setae in the Hyalinoeciinae and presence of single strap-like branchiae in both subfamilies demonstrates the ancestral state of the single strap-like type.

45. Origin of branchiae relatively late (after setiger 10) (0), early (setiger 1–9) (1). Fauchald (1982a) considered the start of branchiae 'on or after setiger 5 but before setiger 10' as plesiomorphic and '(a) on or before setiger 4 (b) after setiger 10' as apomorphic. Some support for this reasoning is found in ontogeny, in that larval branchiae in some species appear at setiger 6 and later spread anteriorly and posteriorly (see p. 20). However, the late occurrence of branchiae in the Hyalinoeciinae (when they are present) and some members of the Onuphinae is here taken as an indication of plesiomorphy.

46. Proximal origin of Mx II and Mx III equal (0), Mx III more anterior (1). The common proximal origin of Mx II and Mx III is found in members of both subfamilies and thought to represent the ancestral condition, while Mx III starting at a more anterior level is thought to be derived.

Relationships Within the Onuphidae

The relationships within the Onuphidae are depicted in a Wagner tree (Fig. 37) and summarized in Table 3. The family includes about 220 species, here placed in 22 genera and considered a monophyletic group with the autapomorphies of possession of frontal palps [1 (number indicates character discussed above—apomorphic state)] and antennae with ceratophores (2). Frontal palps are reduced or absent in *Leptoecia* and *Neonuphis* but this is interpreted as secondary loss as a result of neoteny. The family can be divided into two groups, based on conservative characters, and two subfamilies are erected: Onuphinae and Hyalinoeciinae. The parapodia of Onuphinae generally have notosetae; subacicular hooks are in a ventral position and lower limbate setae are absent posterior to the origin of the former (3); they have four anal cirri; immature eggs have two strings of nurse cells (31) and the primary envelope of mature eggs is smooth. In the Hyalinoeciinae notosetae are absent (4); subacicular hooks are in a median position in the fascicle (5) and lower limbate setae continue to the end of the body; they have two anal cirri (32); nurse cells occur in a single cluster and the primary envelope of eggs is pitted (33).

Relationships within the Hyalinoeciinae. The Hyalinoeciinae consists of about 50 known species, most of them of small size and living at great depths. Some members display neotenic characters, e.g. reduction and loss of frontal palps, and loss of tentacular cirri and

branchiae. Much of this analysis is based on the characteristic tubes that the individual groups construct.

The Hyalinoeciinae falls into two groups: the *Nothria* group and the *Hyalinoecia* group. In members of both groups, the first setiger and its pair of parapodia are enlarged. The latter have claw-like hooks, allowing the animals to be mobile and to pull their protective tubes around with them (Fauchald & Jumars, 1979). *Nothria* and *Anchinotheria* share the scoop-shaped pectinate setae (22) and maxilla III which is distally shorter than maxilla II (23), two characters which are unique within the Eunicida. In discussing the relations among *Nothria* and *Paradiopatra* (= *Anchinotheria*), Fauchald (1982a) considered the short tubes and foliose presetal lobes of *Nothria* as apomorphic conditions. The short tubes of *Nothria* are characteristic and unique, as is their method of construction which renders them flat and smooth (24). Foliose presetal lobes are found in all Hyalinoeciinae except *Anchinotheria*, where they may have been secondarily lost. This loss may represent an apomorphic rather than a plesiomorphic condition. However, the state cannot be definitely assigned and thus the character has not been used. Two species of *Anchinotheria* have dichotomously branched branchiae (25), which is unique.

The loss of tentacular cirri (11) and the construction of clear tubes, secreted completely by its inhabitant without addition of foreign materials (26), are the apomorphies that define the *Hyalinoecia* group. The round, quill-like tubes with internal valves are a characteristic of *Hyalinoecia* (27). *Neonuphis*, *Leptoecia* and presumably *Hyalospinifera* share the possession of maxillae I to III with extremely large cavity openings (28), and the absence of Mx V (29). The three genera occur in abyssal depths and are poorly known. *Neonuphis* constructs round tubes without lateral supports, while both *Leptoecia* and *Hyalospinifera* construct tubes with secreted lateral supporting rods (30). The absence of frontal palps in *Leptoecia* and *Neonuphis* is considered a secondary loss.

Relationships within the Onuphinae. The Onuphinae is by far the more speciose subfamily, with approximately 170 species in 17 genera. Although the individual genera can be satisfactorily defined by autapomorphic characters and grouped into larger units on morphological and ecological characteristics, it is difficult to define these larger units by unequivocal synapomorphies. The genera fall into two broad groups: the *Diopatra* group and the *Onuphis* group.

Members of the *Diopatra* group have representatives at all depths and share a number of characters. The anterior three to five pairs of parapodia are directed anteroventally, the tubes have a parchment-like lining, an additional jaw piece, maxilla VI, and bifid postsetal lobes occur in some species. However, these characters are either ancestral and found already in the Eunicidae, or specialized but not present in all members. The best represented derived character (6) is the presence of two rows of spines on the anterior hooks, found in all but one species of the *Rhamphobrachium* complex and in

some members of *Diopatra*, *Epidiopatra* and *Paradiopatra*.

The *Diopatra* group is here considered to consist of *Notonuphis*, the *Diopatra* complex, the *Rhamphobrachium* complex, and *Americonuphis*. *Notonuphis* is the only onuphine that lacks notosetae (4) and that has maxillae with Mx II and Mx III originating at the same point. The former character is

here interpreted as having evolved parallel to the Hyalinoeciinae, while the latter is taken as a retained plesiomorphic state. *Notonuphis* lacks tentacular cirri (11), a character that has evolved independently several times in the family.

Paradiopatra, *Diopatra* and *Epidiopatra* make up the *Diopatra* complex. Some members of all three genera have branchiae limited to their anterior region (7) and

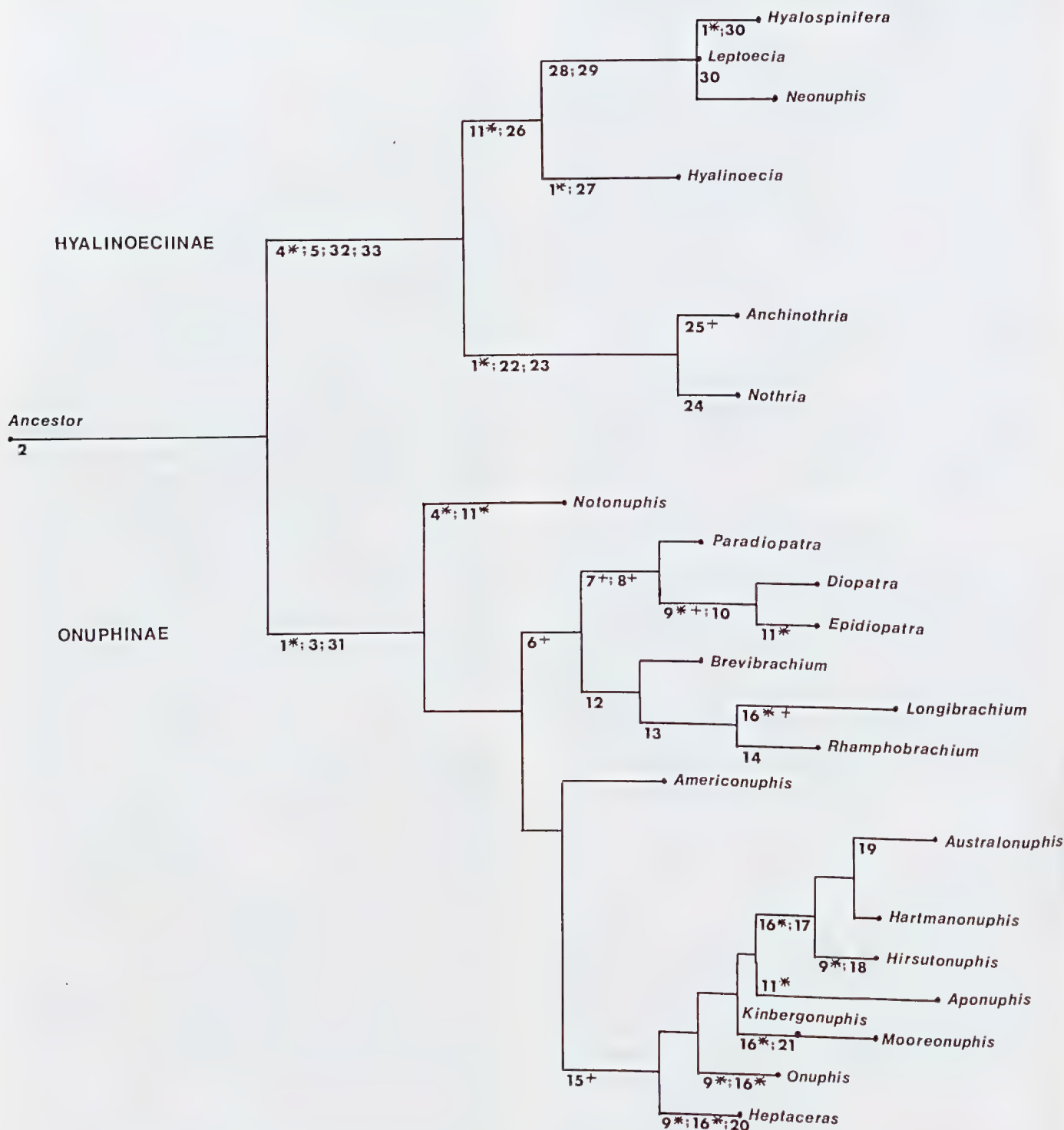


Fig. 37. Wagner tree of Onuphidae computed on basis of 46 characters; overall consistency 0.48 (total length of tree = 92.0). Horizontal lines between linkage levels drawn in proportion to evolutionary distances. All-primitive Ancestor at left; taxa on right more derived. Numbers refer to apomorphic characters (1–33) described in text. Characters 34–46 with widespread apomorphic states not indicated here. * = parallelism; + = character not present in all species.

lateral projections on their ceratophores (8), characters which are not found in any other genera. The puzzling aspect of the lateral projections is their presence in so few species. Anterior hooks with long pointed hoods are present in all species of *Notonuphis*, *Paradiopatra*, some species of *Diopatra*, *Epidiopatra* and some *Hyalinoeciinae*. This type of hood was considered apomorphic by Fauchald (1982a). Long pointed hoods as well as short blunt hoods occur in the Eunicidae so that the state of this character cannot be determined.

Diopatra and *Epidiopatra* share the possession of spiral branchiae (10) and some species of both genera have ceratophores with many rings (9). The former character is unique while the latter character is very plastic and has been attained in a number of genera. *Diopatra* is highly specialized in having well developed sensory buds on its antennae, and almost circular nuchal grooves. *Epidiopatra* lacks tentacular cirri (11); some of its species live in deep water and construct completely organic tubes, suggesting a long independent evolution from its sister group *Diopatra*.

Members of the *Rhamphobrachium* complex share the possession of prolonged modified parapodia which reach their maximum development in species of *Longibrachium*. These parapodia bear long protrusible hooks, the shafts of which extend in long setal sacs in the body cavity (12). In *Brevibrachium* the setal sacs are relatively short (to setiger 5), while in *Longibrachium* and *Rhamphobrachium* they extend to setiger 20–70, representing an extreme specialization (13). Although species of *Brevibrachium* and *Longibrachium* share some features (hooks with immovable spines and similar subacicular hooks), the few species display a great variation of morphology, marking them as survivors of a plastic group. One species of *Longibrachium* has a small maxilla V and lacks Mx VI (16). This state is typical for the *Onuphis* group, and is thought to have evolved independently in *L. atlanticum*. Species of *Rhamphobrachium* are more numerous and morphologically very similar to each other, giving the impression of a more general but successful genus. This is also borne out by their hooks which are very uniform in morphology and unique in having moveable spines (14).

Americonuphis is the genus with the fewest derived characters and is reminiscent of the Eunicidae with its collar-like peristomial fold and posterior emergence of tentacular cirri. Its anterior parapodia are positioned very far ventrally, a condition that is approached in species of the *Rhamphobrachium* complex. It shares the possession of a Mx VI with members of *Longibrachium* and *Rhamphobrachium* (R.) but lacks the prolonged anterior hooks of the *Rhamphobrachium* complex.

Most members of the *Onuphis* group are characterized by the anterolateral to -dorsal direction of the anterior three to eight pairs of parapodia (15) and small maxillae V (16). The former character is best developed in *Australonuphis*, *Hartmanonuphis*, *Hirsutonuphis*, *Heptaceras*, some species of *Onuphis* and *Kinbergonuphis*. It is not obvious in some small

species of *Onuphis*, *Kinbergonuphis* and *Mooreonuphis* and is attributed to the smaller size. The majority of species live in shallow water and have rather temporary tubes, consisting of a thin mucous lining and adhering sand grains or mud.

The *Onuphis* group contains eight genera of which only three (*Australonuphis*, *Hartmanonuphis*, *Hirsutonuphis*) can be defined by a synapomorphy and are here referred to as the *Australonuphis* complex. The nuchal grooves are curved towards the base of the median antenna and are widely separated middorsally. The peristomium lacks a distinct anterior fold, appearing to extend along the nuchal grooves toward the median antenna (17). The parapodia of the anterior five to eight setigers are moderately prolonged and all genera are limited to shallow water habitats. *Hirsutonuphis* is defined by its uniquely shaped and sclerotized maxillary carriers (18). Distally entire subacicular hooks are an autapomorphy of *Australonuphis* (19).

Aponuphis is the only genus in the *Onuphis* group that lacks tentacular cirri (11). Although it resembles *Onuphis* with respect to setal morphology and anteriorly extended prostomium, the two genera do not share any derived characters.

Most of the species of *Kinbergonuphis* and all of *Mooreonuphis* live in shallow water and build temporary tubes. Some species of *Kinbergonuphis* have slightly prolonged parapodia and appear close to the *Australonuphis* complex. Most of the members of the two genera (including the type species) bear the characteristic large median hooks (21). These hooks were reported to be rarely present in *Onuphis* (*O. vexillaria*) and *Sarsonuphis* (= *Paradiopatra*) (*P. lepta*) (Fauchald, 1982a). The former species is here placed with *Kinbergonuphis* for reasons stated in 'Remarks' for the genus *Kinbergonuphis*. My re-examination of *S. lepta* showed that large median hooks are not present in that species, and are thus restricted to *Kinbergonuphis* and *Mooreonuphis*.

Onuphis and *Heptaceras* share setal and prostomial similarities and the possession of many ceratophoral rings (9). The latter genus is unique in having an incised peristomium (20). *Heptaceras* and some species of *Onuphis* share the beachworm habits of members of the *Australonuphis* complex. They also share some morphological features, such as interramal papillae and dorsal cirri with basal processes, with the latter group. However, the former feature is present in very few species, and the latter is found also in *Longibrachium* and *Americonuphis*, indicating an ancestral state. While members of the *Australonuphis* complex have five to eight pairs of modified parapodia and a very late origin of subacicular hooks, *Heptaceras* and most species of *Onuphis* have only three pairs of modified parapodia and a very early origin of subacicular hooks, both of which may be neotenic features.

Identikit Picture of the Uronuphid

While generalized hypothetical ancestors have no value in considering relationships (Anderson, 1982), the reverse process, tracing the ancestor from a previously accepted phylogeny, is an interesting exercise. In the case of the Onuphidae, where there are two clear cut lineages, one can assume that characters in their plesiomorphic condition in both lineages reflect the state of the ancestor.

The prostomium had five antennae, borne on short ceratophores [9 (number indicates character discussed above)]; two frontal palps (1) and two labial palps. The nuchal grooves were straight, with a small middorsal separation. The peristomium had a distinct anterior fold (17), probably even collar-like, covering the nuchal grooves; tentacular cirri were inserted subdistally (34).

A relatively large number (four or more) pairs of parapodia were modified (35) and directed anteroventrally (15) but not prolonged. These parapodia bore subulate dorsal cirri with embedded notosetae (4) and digitate ventral cirri, followed by glandular pads, the most anterior of which may have had additional reduced cirri (36). Branchiae started either around setiger 6, or more likely relatively late (after setiger 10) (45) and consisted of single, strap-like filaments (44).

All modified parapodia bore compound to pseudocompound, distally bidentate (37), hooded hooks. Flat, pectinate setae (22) and several upper narrow limbate setae were present from setiger 1. It is hypothesized here that the lower setae, from the termination of the hooks to the beginning of the subacicular hooks, consisted of spinigers (38). Most modern onuphids have simple limbate setae in the lower position which, I think, evolved from the spinigers by fusion of the fracture, and are morphologically different from the upper limbate setae. The lower limbate setae were continued till the end of the body (3). Bidentate (19), hooded, subacicular hooks probably started late (after setiger 20) (39). The subacicular hooks were in a ventral position (5), may have started as one per parapodium (40), increasing to two and even three to five subsequently (41).

Mandibles were much like Recent ones. Maxillae II were wide with laterally protruding rami (42); Mx III started proximally at the same level as Mx II (46); Mx V were either relatively large plates or each was separated into two plates (16). The tubes were longer than their inhabitants, consisting of a parchment-like inner layer (24) to which foreign particles may have adhered on the outside.

The animals were probably moderately large; they consisted of a great number of segments (more than 100) (43), and probably lived in shallow coastal waters.

ZOOGEOGRAPHY AND CONCLUSION

Members of the family Onuphidae can be found in all world oceans, at all depths. Although some genera

have a world-wide distribution, and are found from the shallowest to the deepest depths, most have a limited geographic and depth distribution.

The family is much better represented in the southern hemisphere than in the northern. Four genera (*Hartmanonuphis*, *Brevibrachium*, *Notonuphis* and *Neonuphis*) are limited to the southern oceans, and another three (*Australonuphis*, *Heptaceras* and *Hyalospinifera*) have only been reported south of 25°N. On the other hand, only *Aponuphis* and *Americonuphis* are limited to the northern hemisphere. This strong southern representation might suggest a southern centre of origin.

The oldest fossil records of the order Eunicida are from the Ordovician and consist of jaw pieces of a number of now extinct families. Of these, only the Paulinitidae (records till early Triassic) shows strong similarity to the Recent Eunicidae and Onuphidae and can be regarded as their possible ancestor (Kielan-Jaworowska, 1966). Isolated palaeozoic onuphid and eunicid jaw pieces have been reported, and completely fossilized specimens of a eunicid are known from the Upper Carboniferous (Thompson & Johnson, 1977). Considering the similarity of the maxillary apparatuses between some Recent representatives of eunicids and onuphids, it may be impossible to distinguish fossil jaw elements of the two families.

The family Eunicidae is a large and successful group. Some members are burrowers, but most are epifaunal on hard substrates, crawling under rocks, invading crevices, and some constructing tubes.

All parapodia of eunicids are similar, directed ventrally, and allow the animal to crawl in an onychophoran-like manner. The most anterior ventral cirri are conical and are replaced by glandular pads with reduced conical cirri which are in contact with the substratum and aid locomotion. The lower setae consist of a bundle of compound hooks, in addition to which the median and posterior regions have two or more subacicular hooks projecting at an angle, thus making them the most ventral setae and providing the *points d'appui*.

Eunicid tubes, when present, consist of parchment-like material, secreted by the animal, without the incorporation of foreign materials. Most eunicids occur in shallow, quiet waters, are most numerous in warm areas, and have occupied these habitats since the Mesozoic (Kozur, 1971) and probably earlier.

A number of onuphid genera (*Americonuphis*, *Longibrachium*, *Australonuphis*, *Hartmanonuphis*, *Hirsutonuphis*, *Heptaceras*) each with very few, widely geographically separated species, of moderately large to large size, with eunicid-like plesiomorphic characters, may represent the survivors of more ancestral onuphids. These genera are all highly specialized in certain features, which may have removed them from the main stream of onuphid evolution. The present distribution of these genera is consistent with the existence of the southern landmass, Gondwanaland, which lasted at least until the Jurassic (Seyfert & Sirkin, 1973) and

supports the hypothesis of a southern origin of the Onuphidae.

While the earliest onuphids were probably mainly epifaunal on hard substrates, the elaboration of their tubes allowed them to become members of the infauna found mainly in soft substrata and rubble (Fauchald & Jumars, 1979). The ancestral onuphids probably were shallow water inhabitants. Many Recent genera occur from intertidal to great depths, suggesting that the deeper waters were invaded independently several times. The genera *Notonuphis*, *Neonuphis*, *Leptoecia* and *Hyalospiniifera* consist of very few species each and occur in deep, mainly Antarctic waters, indicating that they may be survivors of less successful lines.

One of the most interesting genera is *Diopatra*. It is a speciose genus that is not found beyond shelf depths, while even its sister group, *Epidiopatra*, has deep-water representatives. *Diopatra* has a high number of derived characters which allow it to compete successfully and coexist with eunicids in the warmer, shallow waters to which it is limited.

Most of the remaining genera have world-wide geographic distributions, can be found at all depths, and are relatively speciose. *Paradiopatra*, *Rhamphobrachium*, *Nothria* and *Anchinotria* are largely limited to deeper waters. *Onuphis* and *Kinbergonuphis* have a few deep, but mostly shallow-water species, while *Mooreonuphis* and *Aponuphis* are found only in shallow waters. The latter four genera occur mainly in temperate to warmer waters, with *Onuphis* best represented in the western Pacific, *Kinbergonuphis* in the western Atlantic Ocean and *Mooreonuphis* restricted to the Americas. These three genera consist of many closely related, small-sized species, living in thin, temporary tubes. The individual species have relatively limited geographic distributions and may be the result of comparatively recent speciation after reinvading the shallow-water habitats.

While the onuphids have a very similar body plan, jaw apparatus and probably diet to the eunicids, it is mainly the development of more elaborate sensory structures and the specialization of their parapodia that allowed them to compete successfully in habitats where eunicids were already established, and to invade new habitats. The eunicid antennae are short and lack ceratophores, while most onuphids have muscular ceratophores that allow the styles to be well controlled and participate in feeding (Fauchald & Jumars, 1979: fig. 15) and in new activities, such as the selection and manipulation of foreign particles to construct more elaborate tubes (Linville, 1903). The nuchal grooves are covered by the collar-like peristomium in eunicids while they are exposed in most onuphids. The separation of the frontal palps and the more anterior position of the tentacular cirri in onuphids add more sensory structures to the head region.

Another focal point of the onuphid radiation was the modification of the anterior parapodia. They became strengthened for burrowing (beachworms), prolonged for grasping (*Rhamphobrachium*), or enlarged

(*Hyalinoeciinae*) for better crawling. The setae of these parapodia also became specialized. Most onuphids construct permanent tubes, while some burrowing groups live in a mucus-lined hollow, or temporary tube. The inner lining of the tubes is secreted by the glandular ventral pads. The reduced cirri of the eunicids were lost as a consequence in the truly tubicolous groups and retained only in more mobile groups like the beachworms.

The lower bundle of setae, an important aid in the locomotion of eunicids, became modified in two different ways in the onuphids. In the Onuphinae the lower bundle was lost. It is hypothesized that this allowed the subacicular hooks more space, so that they could get a better hold on the inside walls of the tube and act like the uncini of the sedentary tubicolous families. The start of the uncini-like hooks shifted more anteriorly in most onuphines, thus allowing a greater part of the body to grip the tube. The hyalinoeciines retained the lower bundle of setae and adopted the juvenile position of the subacicular hooks in a median position in the fascicle parallel to the acicula. The animals have become mobile through the remarkable development of the first and sometimes second pair of parapodia. These have been greatly enlarged; even the first setiger is enlarged to accommodate the better developed muscles and longer setal sacs. The enlarged parapodia are analogous to the legs of caterpillars, as they crawl around, pulling their protective tube with them.

The hyalinoeciines adopted various ways to overcome the absence of ventral subacicular hooks. Species of *Hyalinoecia* have well developed longitudinal muscles and their body is circular in transverse section (Fig. 2f). The body is closely appressed to the walls of the tube and the whole setal fascicle seems to provide the *points d'appui*. Most of the remaining genera of Hyalinoeciinae have poorly developed longitudinal muscles giving their body an oval shape in transverse section (Fig. 2e). The animals construct flattened tubes to accommodate the oval shape and seem to offset the poor muscular system by a shortened body.

As mentioned above, the reproductive strategies of onuphids are not well known. The large eunicid-like *Americanuphis* spawn large numbers of eggs, which develop in huge egg masses, while species of *Australonuphis* produce even greater numbers of eggs and may be free-spawning. The latter strategies are similar to those of members of the Eunicidae (see Richards, 1967) and can be considered ancestral, thus supporting the conclusions based on the morphological and ecological information.

Most genera have smaller numbers of eggs, which are often brooded in the parental tube. This type of reproduction and development was a preadaptation for invading the deeper waters and probably played an important role in the radiation of the onuphids.

It is concluded that the plasticity of the anterior parapodia and their setae, together with the elaboration of palps and antennae, played a major part in the

radiation of the Onuphidae. The resultant specializations allowed the group to invade the infauna, or provided greater efficiency where the epifaunal habitat was maintained. The tubicolous life allowed for brood care in the parental tube, thus opening the way to the deeper waters. While the onuphids probably evolved in the southern, shallow, warmer waters, they radiated world-wide, inhabiting all depths, and some lines may at present be diversifying in the shallow waters of the northern hemisphere.

ACKNOWLEDGEMENTS. I sincerely thank my supervisor and friend, Noel N. Tait (MU), for his continued support and encouragement.

This study could not have been carried out without the generous help with loans and/or gifts of specimens by the following individuals: Susan J. Williams (AHF); Pat Hutchings (AM); David George and Alex Muir (BMNH); R. Anthony Savill (CM); Herbert W. Levi, John M. Hunter and Ardis B. Johnston (MCZ); J. Renaud-Mornant (MNHP); Suzanne Boyd and Robin Wilson (NMV); P. K. Probert (NZOI); J. B. Jillett (PML); Patricia Mather (QM); Jacob van der Land (RNH); G. A. Knox and Graham Fenwick (UC); Stephen L. Gardiner (UNC); Julie Bailey-Brock (UNH); Marian H. Pettibone and Kristian Fauchald (USNM); Eivind Oug (UT); Loiset Marsh (WAM); G. Hartwich (ZMB); Gesa Hartmann-Schröder (ZMH); Tor A. Bakke and Inger Winsnes (ZMO).

For assistance with scanning electron microscopy and photography I am grateful to Suzanne F. Doyle and Jenny Norman (MU).

Special thanks are due to Marian H. Pettibone (USNM) for her generous help, encouragement, advice and review of the manuscript. I thank Walter Ivantsoff (MU) for translations and George M. McKay (MU) for allowing me to use his unpublished Wagner tree analysis program. Kristian Fauchald (USNM), Gesa Hartmann-Schröder (ZMH), Pat Hutchings (AM) and John R. Paxton (AM) gave critical reviews of the manuscript; to all go my thanks.

The work was supported by a Commonwealth Postgraduate Research Award and Macquarie University Research Grants. Support for a visit to the Western Australian Museum was provided through a grant-in-aid by the Trustees of the Australian Museum.

References

- Allen, M. J., 1959. Embryological development of the polychaetous annelid, *Diopatra cuprea* (Bosc). The Biological Bulletin of the Marine Biological Laboratory Woods Hole 116: 339-361.
- Amoureux, L., 1972. Annélides polychètes recueillies sur les pentes du talus continental, au large de la Galice (Espagne). Campagnes 1967 et 1968 de la "Thalassa". Cahiers de Biologie Marine 13: 63-89.
- 1977. Annélides polychètes errantes recueillies sur les pentes du talus continental, à l'entrée de la Manche, avec la description de deux espèces nouvelles. Campagne 1973 de la "Thalassa". Cahiers de Biologie Marine 18: 391-411.
- 1982. Annélides polychètes recueillies sur la pente continentale de la Bretagne à l'Irlande, campagne 1973 de la "Thalassa" (suite et fin) avec la description de quatre espèces nouvelles pour la science. Cahiers de Biologie Marine 23: 29-51.
- Anderson, D.T., 1982. Origins and relationships among the animal phyla. Proceedings of the Linnean Society of New South Wales 106(2): 151-166.
- Andrews, E. A., 1891a. Reproductive organs of *Diopatra*. Journal of Morphology 5:113-124.
- 1891b. Report upon the Annelida Polychaeta of Beaufort, North Carolina. Proceedings of the United States National Museum 14: 277-302.
- Annenkova, N.P., 1946. New species of Polychaeta from the Arctic Ocean. In 'Works of the drifting ice-expedition in the central Arctic Ocean in the Ice-Breaking Steamer *G. Sedov*, 1937-1940' (ed. V.K. Buinitski): 185-188. Akademia Nauk SSSR, Moscow. (In Russian.)
- 1952. New species of polychaetous annelids (Polychaeta). Trudy Zoologicheskogo Instituta Azerbaidzhanskii filial Akademia Nauk SSSR 12: 148-154. (In Russian.)
- Audouin, J.V. & H. Milne Edwards, 1833. Classification des annélides, et description de celles qui habitent les côtes de la France. Annales des Sciences Naturelles (Paris) (1) 29: 195-269.
- Augener, H., 1906. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and the Caribbean Sea, and on the east coast of the United States, 1877 to 1880, by the U.S. Coast Survey Steamer "Blake", Lieut. Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. 42. Westindische Polychaeten. Bulletin of the Museum of Comparative Zoology at Harvard College 43(4): 91-196.
- 1918. Polychaeta. In 'Beiträge zur Kenntnis der Meeresfauna West-Afrikas' (ed. W. Michaelsen). Vol. 2(2): 67-625. Friedrichsen & Co., Hamburg.
- 1924. Papers from Dr. Th. Mortensen's Pacific Expedition 1914-16. 18. Polychaeta II. Polychaeten von Neuseeland. I. Errantia. Videnskabelige Meddelelser fra Dansk naturhistorisk Förening i Kjøbenhavn 75: 241-441.
- Baird, W., 1870. Remarks on several genera of annelides belonging to the group Eunicea with a notice of such species as are contained in the collection of the British Museum and a description of some others hitherto undescribed. Journal of the Linnean Society of London 10: 341-361.
- Bellan, G., 1964. Contribution à l'étude systématique, bionomique et écologique des annélides polychètes de la Méditerranée. Recueil des Travaux, Station Marine d'Endoume, Bulletin 33: 1-371.
- Bergmann, W., 1903. Untersuchungen über die Eibildung bei Anneliden und Cephalopoden. Zeitschrift für wissenschaftliche Zoologie 73:277-301.
- Berkeley E. & C. Berkeley, 1938. *Rhamphobranchium longisetosum*, sp. n., with some observations on the regeneration of the specialized anterior setae. Annals and Magazine of Natural History (London), (11) 1: 428-435.
- 1939. On a collection of Polychaeta, chiefly from the west coast of Mexico. Annals and Magazine of Natural History (London) (11) 3: 321-346.
- 1941. On a collection of Polychaeta from southern California. Bulletin of the Southern California Academy of Sciences 40: 16-60.
- Blainville, H. de, 1828. Ver. In 'Dictionnaire des sciences naturelles, dans lequel on traite méthodiquement des différents êtres de la nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connoissances, soit relativement à l'utilité qu'en peuvent retirer la médecine, l'agriculture, le commerce et les arts. Suivi d'une biographie des plus célèbres naturalists.' Vol. 57: 1-628. Levrault, Strasbourg.
- Blake, J.A., 1975. The larval development of Polychaeta from

- the northern California coast. II. *Nothria elegans* (Family Onuphidae). *Ophelia* 13: 43-61.
- Carrasco, F.D., 1983. Description of adults and larvae of a new deep water species of *Hyalinoecia* (Polychaeta, Onuphidae) from the southeastern Pacific Ocean. *Journal of Natural History* 17: 87-93.
- Castelli, A., 1982. *Onuphis falesia*, a new species of Onuphinae (Polychaeta, Eunicidae). *Bollettino di Zoologia* 49(1-2): 45-49.
- Chamberlin, R.V., 1919. The Annelida Polychaeta. *Memoirs of the Museum of Comparative Zoology at Harvard College* 48: 1-514.
- Claparède, E., 1868. Les annélides chétopodes du Golfe de Naples, premier partie. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève* 19(2): 313-584.
- Dales, R.P., 1962. The polychaete stomodeum and the interrelationships of the families of Polychaeta. *Proceedings of the Zoological Society London* 139: 389-428.
- Day, J.H., 1951. The polychaete fauna of South Africa. Part I. The intertidal and estuarine Polychaeta of Natal and Mosambique. *Annals of the Natal Museum* 12(1): 1-67.
- 1960. The polychaete fauna of South Africa. Part 5. Errant species dredged off Cape coasts. *Annals of the South African Museum* 45: 261-373.
- 1967. A monograph on the Polychaeta of southern Africa. Part I. Errantia. *British Museum (Natural History) Publications* 656: 1-458.
- 1973. New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. *National Oceanic and Atmospheric Administration Technical Report National Marine Fisheries Service Circular* 375: i-xiii + 1-140.
- Defretin, R., 1971. The tubes of polychaete annelids. *Comprehensive Biochemistry* 26C: 713-747.
- Desière, M., 1967. Morphologie de l'organe buccal ventral de *Murphysa bellii* (Audouin & Edwards) (Polychète, Eunicidae). *Annales de la Société Royale Zoologique de Belgique (Bruxelles)* 97: 65-90.
- Ehlers, E., 1868. Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt. *Engelmann, Leipzig*, pp. 269-748 (pp. 1-268 of this work were published in 1864).
- 1879. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, by the United States Coast Survey Steamer "Blake", Lieutenant-Commander C. D. Sigsbee, U.S.N., commanding. 4. Preliminary report on the worms. *Bulletin of the Museum of Comparative Zoology at Harvard College* 5: 269-274.
- 1887. Reports on the results of dredging, under the direction of L.F. Pourtales, during the years 1868-1870, and of Alexander Agassiz, in the Gulf of Mexico (1877-78), and in the Caribbean Sea (1878-79), in the U.S. Coast Survey Steamer "Blake", Lieut.-Com. C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. 31. Report on the annelids. *Memoirs of the Museum of Comparative Zoology at Harvard College* 15: 1-335.
- 1897. Polychaeten. In 'Ergebnisse der Hamburger Magalhaenischen Sammelreise' 2(1): 1-148. *Friedrichsen & Co., Hamburg*.
- 1908. Die bodensässigen Anneliden aus den Sammlungen der deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898-1899* 16(1): 1-167.
- Estcourt, I.N., 1966. A new polychaete from Three Kings Islands. *Transactions of the Royal Society of New Zealand. Zoology* 7(15): 205-207.
- Eulenstein, F., 1914. Über Onuphiden der Nordsee. *Wissenschaftliche Meeresuntersuchungen, Abteilung Kiel, neue Folge* 16: 129-172.
- Farris, J.S., 1970. Methods for computing Wagner trees. *Systematic Zoology* 19: 83-92.
- Fauchald, K., 1968. Onuphidae (Polychaeta) from western Mexico. *Allan Hancock Monographs in Marine Biology* 3: 1-82.
- 1970. Polychaetous annelids of the families Eunicidae, Lumbrineridae, Iphitimidae, Arabellidae, Lysaretidae and Dorvilleidae from western Mexico. *Allan Hancock Monographs in Marine Biology* 5: 1-335.
- 1972. Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the eastern Pacific Ocean. *Allan Hancock Monographs in Marine Biology* 7: 1-575.
- 1973. Polychaetes from Central American sandy beaches. *Bulletin of the Southern California Academy of Sciences* 72: 19-31.
- 1974. Deep-water errant polychaetes from Hardangerfjorden, western Norway. *Sarsia* 57: 1-32.
- 1977. The Polychaete Worms. Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County Science Series* 28: 1-188.
- 1980. Onuphidae (Polychaeta) from Belize, Central America, with notes on related taxa. *Proceedings of the Biological Society of Washington* 93(3): 797-829.
- 1982a. Revision of *Onuphis*, *Nothria* and *Paradiopatra* (Polychaeta: Onuphidae) based upon type material. *Smithsonian Contributions to Zoology* 356: i-vi + 1-109.
- 1982b. Description of *Mooreonuphis jonesi*, a new species of onuphid polychaete from shallow water in Bermuda, with comments on variability and population ecology. *Proceedings of the Biological Society of Washington* 95(4): 807-825.
- 1982c. Some species of *Onuphis* (Polychaeta: Onuphidae) from the Atlantic Ocean. *Proceedings of the Biological Society of Washington* 95(2): 238-250.
- 1982d. Two new species of *Onuphis* (Onuphidae: Polychaeta) from Uruguay. *Proceedings of the Biological Society of Washington* 95(1): 203-209.
- 1983. Life diagram patterns in benthic polychaetes. *Proceedings of the Biological Society of Washington* 96(1): 160-177.
- & P.A. Jumars, 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology: an Annual Review (London)* 17: 193-284.
- & D. Hancock, 1981. Deep-water polychaetes from a transect off central Oregon. *Allan Hancock Monographs in Marine Biology* 11: 1-73.
- Fauvel, P., 1916. Deux polychètes nouvelles (*Disoma watsoni* n. sp., et *Hyalinoecia brementi* n. sp.). *Bulletin d'institut océanographique (Monaco)* 316: 1-10.
- 1923. Polychètes errantes. *Faune de France, Paris* 5: 1-488.
- 1928. Annélides polychètes nouvelles du Maroc. *Bulletin de la Société Zoologique de France (Paris)* 53: 9-13.
- 1932. Annelida Polychaeta of the Indian Museum, Calcutta. *Memoirs of the Indian Museum (Calcutta)* 12(1): 1-252.

- Franzén, Å., 1956. On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. *Zoologisce Bidrag Uppsala* 31: 355-482.
- Friedrich, H., 1956. Mitteilungen über neue und wenig bekannte Polychaeten aus Mittel- und Südamerika. *Senckenbergiana Biologica* 37(1/2): 57-68.
- Gallardo, V.A., 1968. Polychaeta from the Bay of Nha Trang, South Viet Nam. NAGA Reports, Scientific Results of Marine Investigations of the South China Sea and the Gulf of Thailand 1959-1961 4(3): 35-279.
- Gardiner, S. L., 1976. Errant polychaete annelids from North Carolina. *Journal of the Elisha Mitchell Scientific Society* 91(3): 77-220.
- Grube, A.-E., 1868. Über eine Reihe neuer Anneliden. Jahresbericht der Schlesischen Gesellschaft für vaterländische Cultur (Breslau) 45: 50-52.
- Haffner, K. von, 1959. Über den Bau und den Zusammenhang der wichtigsten Organe des Kopfendes von *Hyalinoecia tubicola* Malmgren (Polychaeta, Eunicidae, Onuphidiinae), mit Berücksichtigung der Gattung Eunice. *Zoologische Jahrbücher, Abteilung für Anatomie* 77(2): 133-192.
- Hansen, G.A., 1878. Annelider fra den norske Nordhavsexpedition i 1876. *Nyt Magazin for Naturvidenskaberne* (Christiania) 24: 1-17.
- 1882. Recherches sur les annélides, recueillies par M. le professeur Édouard van Beneden pendant son voyage au Brésil et à la Plata. Mémoires couronnés et mémoires des savants étrangers publiés par l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique (Bruxelles) 44(3): 1-29.
- Hartman, O., 1944. Polychaetous annelids. Part 5. Eunicea. *Allan Hancock Pacific Expeditions* 10: 1-238.
- 1945. The marine annelids of North Carolina. *Duke University Marine Station Bulletin* 2: 1-54.
- 1951. The littoral marine annelids of the Gulf of Mexico. *Publications of the Institute of Marine Science (Port Aransas)* 2(1): 7-124.
- 1959. Catalogue of the polychaetous annelids of the world. *Allan Hancock Foundation Occasional Paper* 23: 1-628.
- 1965. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Allan Hancock Foundation Occasional Paper* 28: 1-378.
- 1967a. Larval development of benthic invertebrates in Antarctic seas: early development of *Nothria notialis* (Monro) and *Paronuphis antarctica* (Monro) in Bransfield Strait, Antarctic Peninsula. *Proceedings of the Symposium on Pacific-Antarctic Sciences. JARE Scientific Reports, Special Issue 1*: 205-208.
- 1967b. Polychaetous annelids collected by the USNS *Eltanin* and *Staten Island* cruises, chiefly from Antarctic seas. *Allan Hancock Monographs in Marine Biology* 2: 1-387.
- & K. Fauchald, 1971. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. Part 2. *Allan Hancock Monographs in Marine Biology* 6: 1-327.
- Hartmann-Schröder, G., 1960. Zur Polychaeten-Fauna von Peru, Part I. Beiträge zur Neotropischen Fauna 2: 1-44.
- 1965. Die Polychaeten des Sublitorals. In 'Zur Kenntnis des Sublitorals der chilenischen Küste unter besonderer Berücksichtigung der Polychaeten und Ostracoden (mit Bemerkungen über den Einfluss sauerstoffarmer Strömungen auf die Besiedlung von marinen Sedimenten)' (G. Hartmann & G. Hartmann-Schröder). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 62: 59-305.
- 1967. Feinbau und Funktion des Kieferapparates der Euniciden am Beispiel von *Eunice (Palola) sicilensis* Grube (Polychaeta). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 64: 5-27.
- 1975. Polychaeten der Iberischen Tiefsee, gesammelt auf der 3. Reise der METEOR im Jahre 1966. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 72: 47-73.
- Heider, K., 1925. Über *Eunice*, Systematisches, Kiefersack, Nervensystem. *Zeitschrift für wissenschaftliche Zoologie* 125: 55-90.
- Hennig, W., 1966. *Phylogenetic systematics*. University of Illinois Press, Urbana, pp. 269.
- Hoagland, R. A., 1920. Polychaetous annelids collected by the United States Fisheries Steamer "Albatross" during the Philippine Expedition of 1907-1909. *Bulletin of the United States National Museum* 100 1(9): 603-635.
- Hobson, K.D., 1971. Some polychaetes of the superfamily Eunicea from the North Pacific and North Atlantic Oceans. *Proceedings of the Biological Society of Washington* 83: 527-544.
- Hove, H.A. ten, 1984. Towards a phylogeny in serpulids (Annelida; Polychaeta). In 'Proceedings of the First International Polychaete Conference, Sydney' (ed. P.A. Hutchings): 181-196. The Linnean Society of New South Wales, Sydney.
- Imajima, M., 1960. Description of a new polychaete, *Nothria shirikishinaensis* n. sp. of the family Eunicidae. *Publications of the Seto Marine Biological Laboratory* 8(1): 55-58.
- Intes, A. & P. Le Loeuff, 1975. Les annélides polychètes de Côte d'Ivoire. I.-Polychètes errantes-compte rendu systématique. *Cahiers de la Office de la Recherche Scientifique et Technique des outre mer (Oceanographie)* 13(4): 267-321.
- Jeuniaux, C., 1975. Principes de systématique biochimique et application à quelques problèmes particuliers concernant les aschelminthes, les polychètes et les tardigrades. *Cahiers de Biologie Marine* 16: 597-612.
- Johnson, H.P., 1901. The Polychaeta of the Puget Sound region. *Proceedings of the Boston Society of Natural History* 29: 381-437.
- Johnston, G., 1865. A catalogue of the British non-parasitical worms in the collection of the British Museum. London, pp. 366.
- Just, E.E., 1922. On rearing sexually mature *Platynereis megalops* from eggs. *American Naturalist* 56: 471-478.
- Kielan-Jaworowska, Z., 1966. Polychaete jaw apparatuses from the Ordovician and Silurian of Poland and a comparison with modern forms. *Palaeontologia Polonica* 16: 1-152.
- Kinberg, J.G.H., 1865. *Annulata nova*. Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar (Stockholm) 21: 559-574.
- Kirkegaard, J.B., 1980. Abyssal benthic polychaetes from the northeast Atlantic Ocean, southwest of the British Isles. *Steenstrupia, Zoological Museum, University of Copenhagen* 6(8): 81-98.
- Knox, G.A. & K. Hicks, 1973. The polychaetes of New Zealand. Part 5. Onuphidae. *Journal of the Royal Society of New Zealand* 3(2): 281-294.
- Kozur, H., 1971. Die Eunicida und Phyllodocida des Mesozoikums. *Freiberger Forschungshefte (C)* 267: 73-111.
- Krishnamoorthi, B., 1963. Volume regulation in eggs, larvae and adults of a brackish-water polychaete, *Diopatra*

- variabilis* (Southern). Proceedings of the Indian Academy of Sciences B57: 1275-1289.
- Krishnan, G., 1936. The development of *Diopatra variabilis* (Southern). Zeitschrift für wissenschaftliche Zoologie 147: 513-525.
- Kucheruk, N.V., 1977. On the specific composition and distribution of the deep-sea genus *Paraonuphis* (sic) (Polychaeta, Eunicidae). Trudy Institutyi Okeanologii Akademia Nauk SSSR 108: 44-51. (In Russian.)
- 1978. Deep-water Onuphidae (Polychaeta) from the collections of the 16th cruise of the R/V *Dmitry Mendeleev* (to the generic classification of the family Onuphidae). Trudy Institutyi Okeanologii Akademia Nauk SSSR 113: 88-106. (In Russian.)
- 1979a. New species of the family Onuphidae (Polychaeta) from the Pacific. Zoologicheskyy Zhurnal, Akademia Nauk SSSR 58: 1227-1230. (In Russian.)
- 1979b. A new genus and species of polychaetes (Onuphidae). Zoologicheskyy Zhurnal, Akademia Nauk SSSR 58: 1585-1587. (In Russian.)
- Langerhans, P., 1880. Wurmfauna von Madeira. Zeitschrift für wissenschaftliche Zoologie 33: 267-316.
- Lieber, A., 1931. Zur Oogenese einiger Diopatraarten. Zeitschrift für wissenschaftliche Zoologie 138: 580-649.
- Linville, H.R., 1903. The natural history of some tube-forming annelids (*Amphitrite ornata*, *Diopatra cuprea*). In 'Mark Anniversary Volume' (ed. G.H. Parker): 225-235. Henry Holt & Co, New York.
- Malmgren, A.J., 1866. Annulata Polychaeta Spetsbergiae, Groenlandiae, Islandiae et Scandinaviae hactenus cognita. Frenckelliana, Helsingfors, pp. 127.
- Mangum, C. & W.R. Rhodes, 1970. The taxonomic status of quillworms, genus *Hyalinoecia* (Polychaeta: Onuphidae), from the North American Atlantic continental slope. Postilla (Yale Peabody Museum of Natural History) 144: 1-13.
- Marenzeller, E. von, 1879. Süd-japanische Anneliden. I. Dankschrift der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften (Wien) 41(2): 109-152.
- 1886. Poriferen, Anthozoen, Ctenophoren und Würmer von Jan Mayen. In 'Die internationale Polarforschung 1882-1883. Die österreichische Polarstation Jan Mayen ausgerüstet durch seine Excellenz Graf Hanns Wilczek geleitet vom K.K. Corvetten-Capitän Emil Edlen von Wohlgemuth'. Beobachtungs-Ergebnisse herausgegeben von der Kaiserlichen Akademie der Wissenschaften (Wien) 3(B): 9-24.
- McIntosh, W.C., 1885. Report on the Annelida Polychaeta collected by the H.M.S. *Challenger* during the years 1873-76. Report on the Scientific Results of the Voyage of H.M.S. *Challenger* during the Years 1873-1876 under the Command of Captain George S. Nares, R. N., F.R.S. and the Late Captain Frank Tourle Thomson, R.N., Zoology 12(34): 1-554.
- 1903. Notes from the Gatty Marine Laboratory, St. Andrews, no. 25. Annals and Magazine of Natural History (London) (7) 12: 128-166.
- 1910. A monograph of the British annelids. Polychaeta. Syllidae to Ariciidae. Ray Society (London) 2(2): 233-524.
- Mill, P.J., 1978. Sense organs and sensory pathways. In 'Physiology of annelids' (ed. P.J. Mill). Academic Press, London, pp. xvi + 683.
- Milne Edwards, H., 1838. Les annélides. In 'Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels; enfin, l'exposition des principes fondamentaux de la zoologie' (J.B.P.A. de Lamarck), 2nd ed. by G.P. Deshayes & H. Milne Edwards, vol. 5: 1-699. Baillière, Paris.
- Monro, C.C.A., 1924. On the post-larval stages of *Diopatra cuprea*, Bosc, a polychaetous annelid of the family Eunicidae. Annals and Magazine of Natural History (London) (9) 14: 193-199.
- 1930. Polychaete worms. Discovery Reports 2: 1-222.
- 1933. The Polychaeta Errantia collected by Dr. C. Crossland at Colon in the Panama region and the Galapagos Islands during the expedition of the S.Y. St. George. In 'Proceedings of the General Meetings for Scientific Business of the Zoological Society of London'. London, pp. 96.
- 1937. Polychaeta. The John Murray Expedition 1933-34 Scientific Reports 4(8): 243-321.
- Moore, J.P., 1903. Polychaeta from the coastal slope of Japan and from Kamchatka and Bering Sea. Proceedings of the Academy of Natural Sciences of Philadelphia 55(2): 401-490.
- 1911. The polychaetous annelids dredged by the U.S.S. "Albatross" off the coast of southern California in 1904: III. Euphrosynidae to Goniadidae. Proceedings of the Academy of Natural Sciences of Philadelphia 63: 234-318.
- Müller, O.F., 1776. Zoologica Danicae prodromus seu animalium Daniae et Norvegiae indigenarum characteres, nomina et synonyma imprimis popularium. Havniae, pp. xxxii + 274.
- Nelson, G.J., 1978. Ontogeny, phylogeny, paleontology and the biogenetic law. Systematic Zoology 27: 324-345.
- Orensanz, J.M., 1974. Los anélidos poliquetos de la provincia biogeográfica Argentina. V. Onuphidae. Physis (Buenos Aires) A33(86): 75-122.
- Paxton, H., 1979. Taxonomy and aspects of the life history of Australian beachworms (Polychaeta: Onuphidae). Australian Journal of Marine and Freshwater Research 30: 265-294.
- 1980. Jaw growth and replacement in Polychaeta. Journal of Natural History 14: 543-546.
- 1986. Revision of the *Rhamphobranchium* complex (Polychaeta: Onuphidae). Records of the Australian Museum 38(2): 75-104.
- Revision of the Genus *Diopatra* (Polychaeta: Onuphidae). (In preparation).
- Onuphidae (Polychaeta) from the Australia-New Zealand Region. (In preparation).
- Pettibone, M.H., 1963. Marine polychaete worms of the New England region. I. Aphroditidae through Trochochaetidae. Bulletin of the United States National Museum 227(1): 1-356.
- 1970. Polychaeta Errantia of the Siboga-Expedition. Part IV: Some additional polychaetes of the Polynoidae, Hesionidae, Nereidae, Goniadidae, Eunicidae, and Onuphidae, selected as new species by the late Dr. Hermann Augener with remarks on other related species. Siboga-Expedition Monographie 24(1d): 199-270.
- Pflugfelder, O., 1929. Histogenetische und organogenetische Prozesse bei der Regeneration polychaeter Anneliden. I.

- Regeneration des Vorderendes von *Diopatra amboinensis* Aud. et M. Edw.. Zeitschrift für wissenschaftliche Zoologie 133: 121-210.
- Pourtales, L.F. de, 1869. Contributions to the fauna of the Gulf Stream at great depths. Bulletin of the Museum of Comparative Zoology at Harvard College 1: 103-120.
- Rangarajan K. & S. Mahadevan, 1961. On a new species of *Nothria* Malmgren (Polychaeta, Annelida) from the Gulf of Mannar. Journal of the Marine Biological Association of India 4: 179-185.
- Richards, T. L., 1967. Reproduction and development of the polychaete *Tauronereis rudolphi*, including a summary of development in the superfamily Eunicea. Marine Biology 1: 124-133.
- Rioja, E., 1918. Datos para el conocimiento de la fauna de anelidos poliquetos del Cantabrico. Trabajos de museo nacional de ciencias naturales (Madrid) (Zoologica) 29: 1-111.
- 1944. Estudios anelidologicos, XI: Notes sobre algunas especies de poliquetos de las costas mexicanas del Pacifico. Anales Instituto Biologica (Mexico) 15: 139-145.
- Rozbaczylo, N. & J.C. Castilla, 1981. *Australonuphis violacea*, a new polychaete (Onuphidae) from the southeast Pacific Ocean. Proceedings of the Biological Society of Washington 94(3): 761-770.
- Saint-Joseph, A. de, 1906. Les annélides polychètes des côtes de France. Annales des Sciences Naturelles (Paris) (9) 3: 145-260.
- Santos, S.L., R. Day & S.A. Rice, 1981. *Onuphis simoni*, a new species of polychaete (Polychaeta: Onuphidae) from South Florida. Proceedings of the Biological Society of Washington 94(3): 663-668.
- Sars, G.O., 1872. Diagnoser af nye Annelider fra Christianiafjorden, efter Professor M. Sars's efterladte Manuskripter. Videnskabsselskabet i Christiania Forhandling 1871: 406-417.
- Sars, M., 1835. Beskrivelser og iagttagelser over nogle mærkelige eller nye i havet ved den Bergenske kyst levende dyr af Polypernes, Acalophernes, Radiaternes, Annelidernes og Molluskernes classer, med en kort oversigt over de hidtil af forfatteren sammesteds fundne arter og deres forekommen. Bergen, pp. xii + 81.
- Schmarda, L.K., 1861. Neue Tubellarien, Rotatorien und Anneliden beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857. Zweite Hälfte. Wilhelm Engelmann, Leipzig, pp. 164.
- Schroeder, P.C. & C.O. Hermans, 1975. Annelida: Polychaeta. In 'Reproduction of Marine Invertebrates' (eds. A.C. Giese & J.S. Pearse). Vol. III Annelids and Echiurans: 1-213. Academic Press, New York.
- Seyfert, C.K. & L.A. Sirkin, 1973. Earth history and plate tectonics, an introduction to historical geology. Harper and Row, New York, pp. viii + 504.
- Shisko, J.F., 1981. Five new polychaetes of the families Eunicidae and Onuphidae, collected in 1975 and 1976 during the southern California Baseline Project. Proceedings of the Biological Society of Washington 94(4): 968-983.
- Smith, B.J. & R.L. Jenz, 1968. Unusual mode of reproduction in a new species of polychaete. Nature 218: 777.
- Thompson, I. & R.G. Johnson, 1977. New fossil polychaete from Essex, Illinois. Fieldiana Geology 33(25): 471-487.
- Treadwell, A.L., 1922. Polychaetous annelids collected at Friday Harbor, state of Washington in February and March, 1920. Publication of the Carnegie Institute of Washington 312: 171-181.
- 1931. Contributions to the biology of the Philippine Archipelago and adjacent regions: four new species of polychaetous annelids collected by the United States Fisheries Steamer Albatross during the Philippine Expedition of 1907-1910. Bulletin of the United States National Museum 100, 6(5): 313-321.
- Uschakov, P.V., 1950. Polychaetous annelids (Polychaeta) of the Sea of Okhotsk. Issledovanii Dal'nevostochnykh morei SSSR 2: 140-324. (In Russian.)
- & B.-L. Wu, 1962. Littoral fauna of polychaete worms of the provinces of Fukian and Chekian. Studio Marine Sinica 1: 89-108. (In Chinese and Russian.)
- Verrill, A.E., 1873. Results of recent dredging expeditions on the coast of New England. American Journal of Science (New Haven) (3) 5: 98-106.
- Voss-Foucart, M.-F., M.-T. Fonze-Vignaux & C. Jeuniaux, 1973. Systematic characters of some polychaetes (Annelida) at the level of the chemical composition of the jaws. Biochemical Systematics 1: 119-122.
- Westheide, W., 1977. Phylogenetic systematics of the genus *Microphthalmus* (Hesionidae) together with a description of *M. hartmanae* nov. sp. In 'Essays on polychaetous annelids in memory of Dr. Olga Hartman' (eds. D.J. Reish & K. Fauchald): 103-113. Allan Hancock Foundation, Los Angeles.
- 1982. *Ikosipodus carolensis* gen. et sp. n., an interstitial neotenic polychaete from North Carolina, U.S.A., and its relationships within Dorvilleidae. Zoologica Scripta 11(2): 117-126.
- & N.W. Riser, 1983. Morphology and phylogenetic relationships of the neotenic interstitial polychaete *Apodotrocha progenerans* n. gen., n. sp. (Annelida). Zoomorphology 103: 67-87.
- Wiley, A., 1905. Report on the Polychaeta collected by Professor Herdman, at Ceylon, in 1902. Supplementary report 30. In 'Report to the government of Ceylon on the pearl oyster fisheries of the Gulf of Manaar with supplementary reports upon the marine biology of Ceylon by other naturalists' (ed. W. A. Herdman). Part 4: 243-324. Royal Society, London.
- Wolf, G., 1976. Bau und Funktion der Kieferorgane von Polychaeten. Private printing, Hamburg, pp. i + 70.
- 1980. Morphologische Untersuchungen an den Kieferapparaten einiger rezenter und fossiler Eunicoidea (Polychaeta). Senckenbergiana Maritima 12(1/4): 1-182.

Accepted 2 December 1985

RECORDS OF THE AUSTRALIAN MUSEUM

VOLUME 38 No. 2

- Revision of the *Rhamphobrachium* complex (Polychaeta: Onuphidae)
HANNELORE PAXTON 75
- A revision of the genus *Euthelepus* (Terebellidae: Thelepinae) PAT HUTCHINGS
and CHRIS GLASBY 105

Revision of the *Rhamphobrachium* Complex (Polychaeta: Onuphidae)

HANNELORE PAXTON

School of Biological Sciences, Macquarie University,
North Ryde, NSW 2113, Australia

ABSTRACT. The *Rhamphobrachium* complex is revised. Three species each are recognized for *Brevibrachium* and *Longibrachium*, of which *B. augeneri* and *L. longipes* are newly described. Two subgenera of *Rhamphobrachium* are established: *R. (Rhamphobrachium)* containing two species, and *R. (Spinigerium)* n. subgen., containing 10 species, of which four [*R. (S.) hutchingsae*, *R. (S.) noeli*, *R. (S.) pettiboneae* and *R. (S.) pyriforme*] are described as new. Three additional species, *R. (S.) bipes*, *R. (S.) brevicornutum* and *R. (S.) cristobalensis*, known only from juveniles, are treated as *incertae sedis*. Keys to adults and descriptions of all species are provided.

PAXTON, HANNELORE, 1986. Revision of the *Rhamphobrachium* complex (Polychaeta: Onuphidae). Records of the Australian Museum 38(2): 75-104.

CONTENTS

INTRODUCTION	76
MATERIALS AND METHODS	76
Key to Genera of <i>Rhamphobrachium</i> Complex	76
Key to Species of <i>Brevibrachium</i>	77
<i>B. capense</i>	77
<i>B. augeneri</i>	77
<i>B. maculatum</i>	79
Key to Species of <i>Longibrachium</i>	80
<i>L. atlanticum</i>	80
<i>L. longipes</i>	81
<i>L. quadripes</i>	83
Key to Species of <i>Rhamphobrachium</i>	84
<i>R. agassizii</i>	85
<i>R. chuni</i>	86
<i>R. longusetosum</i>	88
<i>R. averincevi</i>	89
<i>R. brevibrachiatum</i>	89
<i>R. diversisetisum</i>	92
<i>R. ehlersi</i>	93
<i>R. hutchingsae</i>	94
<i>R. noeli</i>	97
<i>R. pettiboneae</i>	97
<i>R. pyriforme</i>	99
<i>R. verngreni</i>	99

<i>INCERTAE SEDIS</i>	101
? <i>R. bipes</i>	101
<i>R. brevicornutum</i>	102
? <i>R. cristobalensis</i>	102
 <i>ACKNOWLEDGEMENTS</i>	103
 <i>REFERENCES</i>	103

The genus *Rhamphobranchium* was erected by Ehlers, 1887 for his previously described *Onuphis brevibrachiatum* and a new species, *R. agassizii*. The characteristics of the genus were given as three prolonged anterior pairs of parapodia with spiny, recurved hooks. This definition was later broadened by Monro (1937), Estcourt (1966) and Kucheruk (1979a) with the inclusion of species with two pairs of prolonged parapodia (*R. bipes*), with spineless recurved hooks (*R. maculatum*), and with four pairs of prolonged parapodia (*R. quadripes*), bringing the number of nominal species to 17.

Paxton (1986) demonstrated that specimens with two pairs of modified parapodia are juveniles, and that *R. maculatum* and several species with four or five pairs of modified parapodia differ also in a number of additional important characters (types of spines, distal ends of setae, length of setal sacs, prostomial characters, etc.). She restricted the definition of *Rhamphobranchium* to species with three pairs of modified parapodia with three hooks with moveable spines each and long setal sacs (extending to setiger 30–60), and described two new genera, *Brevibranchium* and *Longibranchium*, to accommodate the pre-empted species. She regarded the group as a complex of related genera, with *Brevibranchium* and particularly *Longibranchium* representing specialized survivors of a more plastic group, and *Rhamphobranchium* the most generalized and successful of the three genera.

The aim of this paper is to provide keys and descriptions to all species of the *Rhamphobranchium* complex.

Materials and Methods

The material examined was loaned by and/or is

deposited in the following institutions:

AHF	Allan Hancock Foundation, Los Angeles, Calif., U.S.A.
AM	Australian Museum, Sydney, NSW, Australia
BMNH	British Museum (Natural History), London, U.K.
MU	Macquarie University, North Ryde, NSW, Australia
MCZ	Museum of Comparative Zoology, Cambridge, Mass., U.S.A.
MNHP	Muséum National d'Histoire Naturelle, Paris, France
NMV	Museum of Victoria, Melbourne, Vic., Australia
NZOI	New Zealand Oceanographic Institute, Wellington, New Zealand
PML	Portobello Marine Laboratory, Portobello, New Zealand
QM	Queensland Museum, Brisbane, Qld, Australia
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.
ZMB	Zoologisches Museum, Berlin, E. Germany
ZMH	Zoologisches Institut und Zoologisches Museum, Hamburg, W. Germany

Counts and measurements are of the holotype or only type specimen examined, the range for other specimens examined or reported in the literature are given in parentheses. The body length measurements and numbers of setigers of incomplete specimens are followed by plus signs. Body width (without parapodia) is of setiger 10 unless otherwise stated. Terminology follows Paxton (1986). All keys are for adults only.

Key to Genera of *Rhamphobranchium* Complex

1. Three pairs of modified parapodia (with 3 setae each) with spiny shafts and distally recurved (Fig. 9a). *Rhamphobranchium*
- Four to 5 pairs of modified parapodia (with 4 or more setae each) with spiny shafts, or 3 pairs of modified parapodia with smooth shafts. 2
2. Antennae moderately long, to setiger 6–15; 4 pairs of modified parapodia with single postsetal lobes and setae with spiny shafts and distally curved (Fig. 4c). *Longibranchium*
- Antennae short, to setiger 1; 3–5 pairs of modified parapodia with double postsetal lobes and setae with spiny shafts and distally uni- to tridentate (Fig. 1b) or smooth shafts and distally recurved (Fig. 3d). *Brevibranchium*

Genus *Brevibranchium* Paxton

Brevibranchium Paxton, 1986: 41. Type species: *Rhamphobranchium capense* Day, 1960: 355, by original designation. Gender: neuter.

Diagnosis. Anterior 3–5 pairs of parapodia prolonged, with more than 3 hooks each; hooks smooth, distally recurved, or uni- to tridentate, with 2 rows of immovable spines; setal sacs extending to setiger 4–8.

Remarks. For a full definition of the genus see Paxton (1986).

Key to Species of *Brevibranchium*

1. Branchiae from setiger 2, pectinate filaments (Fig. 1a); anterior 4 pairs of parapodia modified. *B. augeneri*
 —Branchiae from setiger 15–40, single filaments throughout; anterior 3 or 5 pairs of parapodia modified. 2
2. Branchiae from setiger 15–17; 3 pairs of modified parapodia; hooks of modified parapodia spineless, distally recurved (Fig. 2d). *B. maculatum*
 —Branchiae from setiger 30–40; 5 pairs of modified parapodia; hooks of modified parapodia spiny, uni- to tridentate. *B. capense*

Brevibranchium capense (Day)

Rhamphobranchium capense Day, 1960: 355, fig. 11i–l (False Bay, South Africa; 27.5 m); 1967: 418, fig. 17.12g–k (False Bay to eastern Cape, South Africa).—Paxton, 1986: 41 fig. 25a–k (definition of genus).

Material examined. South Africa: False Bay, 34°07.5'S, 18°31'E, 27.5 m, 22 Feb. 1947—3 PARATYPES (BMNH ZK 1961.20.4–7 and ZK 1961.20.13); Algoa Bay, 34°00.4'S, 25°44.5'E, 39 m, 11 Apr. 1954—1 PARATYPE ZK 1961.20.14).

Diagnosis. Anterior 5 pairs of parapodia modified; branchiae from setiger 30–40, single filament throughout; uni- to tridentate hooded spiny hooks on modified setigers; subacicular hooks from setiger 10.

Description. Length of almost complete specimen 34 mm for 78 segments, width about 1.5 mm. Prostomium anteriorly rounded, posterior antennae on median part of prostomium, with ceratophores with 2–3 proximal rings and longer distal ring, styles subulate, short, to setiger 1; small eyespots between bases of posterior and anterior lateral antennae; tentacular cirri subulate, inserted far apart.

Anterior 5 pairs of parapodia modified (Paxton, 1986: fig. 25b,c), with oval presetal lobes on parapodia 1 becoming smaller towards parapodia 5; large subulate postsetal lobes with small ventral accessory lobes. Following parapodia short; low presetal and subulate postsetal lobes, latter reduced to rounded cone from about setiger 12. Dorsal cirri subulate on modified

parapodia, thereafter decreasing in size, small after setiger 10 (Paxton, 1986: fig. 25d); ventral cirri subulate on anterior 5 setigers. Branchiae from setiger 30–40; single, strap-like filaments to near end of body.

Modified parapodia with simple to pseudocompound uni- to tridentate hooded spiny hooks (Paxton, 1986: fig. 25e,f) of varying sizes: 4 largest hooks emerging from small papillae, 4–6 slightly smaller hooks, 4–8 small hooks from ventral pocket of presetal fold. Spines on large hooks closely spaced, length half width of shaft, spines on small hooks far apart, length equalling width of shaft. Hooks of parapodia 1 and 2 bi- to tridentate, ends of hoods bent like claws; smaller hooks of parapodia 3 unidentate, hoods with straight ends, larger hooks as above; all hooks of parapodia 4 and 5 unidentate, hoods without claws. Tips of acicula projecting slightly from setal lobes of parapodia 1 to 5, becoming long and filiform from setiger 6 (Paxton, 1986: fig. 25g). Pectinate setae (comb with 12–16 teeth) and simple limbate setae from setiger 6. Anterior limbate setae with wide blades and filiform tips (Paxton, 1986: fig. 25h,i), becoming slenderer and longer more posteriorly. Two bidentate, usually hooded subacicular hooks (Paxton, 1986: fig. 25j) from setiger 10.

Mandibles calcified, shafts slender, cutting plates with middle notch; maxillae hardly sclerotized; maxillary formula: Mx I = 1 + 1; Mx II = 6 + 6; Mx III = 5 + 0; Mx IV = 5 + 7; Mx V = 1 + 1. Thin mucous tube with adherent fragments of shells, coralline algae and sand (Day, 1960).

Remarks. The anterior hooks were described by Day (1960) as 'pseudocompound' and present on the first 3 setigers. However, they are present on the first 5 setigers, and the paratypes examined from False Bay do not show any fracture, nor did Day indicate any in his illustration (Day, 1960: fig. 11k). A single specimen from Algoa Bay differs in having pseudocompound hooks and lacking spines in the area of the fracture (Paxton, 1986: fig. 25k).

Distribution. False Bay to eastern Cape, South Africa; 12–72 m.

Brevibranchium augeneri n. sp.

Figs 1a–g; 2a,b

Rhamphobranchium chuni (not Ehlers, 1908).—Augener, 1927: 178, fig. 8 (Southeast Australia).

Material examined. Australia: New South Wales: Shelf Benthic Survey sta. III, 1.6 km E of Malabar, 33°58'15"S, 150°17'0"E, 66 m, 30 Jan. 1974—HOLOTYPE (AM W.6268).

Diagnosis. Anterior 4 pairs of parapodia modified; branchiae from setiger 2, reaching maximum of 5 filaments by setiger 12; tridentate hooded spiny hooks on modified setigers; subacicular hooks from setiger 9.

Description. Description based on 1 anterior portion; length 14 mm (26 setigers), width 2 mm. Ceratophores of antennae with 2–3 proximal rings and longer distal article, styles broken off; no eyes visible; tentacular cirri broken off, bases far apart.

Anterior 4 pairs of parapodia modified, with low presetal lobes, postsetal lobes broken off. Following parapodia short; low presetal and digitate postsetal lobes (Fig. 1a), reduced to rounded cone at end of fragment (setiger 26). Dorsal cirri initially subulate, later digitate; ventral cirri subulate on anterior 4 setigers. Branchiae as single filaments from setiger 2, reaching maximum of 5 filaments by setiger 12.

Modified parapodia with 4–5 tridentate hooded spiny hooks. Secondary and tertiary teeth vary from large (Fig. 1b) to very short (Fig. 1c). Spines on hooks closely spaced, length half to two-thirds width of shaft. Hooks of setiger 1 and 2 simple, those of 3 and 4 weakly pseudocompound, spines absent in area of fracture. Tips of acicula projecting slightly from setal lobes of parapodia 1 to 4, becoming long and filiform from setiger 5 (Fig. 1d). Pectinate setae (oblique comb with 15–20 teeth) (Fig. 1e) and simple limbate setae from setiger 5. Upper and median limbate setae weakly winged (Fig. 1f), lower limbate setae cultriform (Fig. 1g). Two bidentate, usually hooded subacicular hooks (Fig. 2a) from setiger 9.

Mandibles with slender shaft, calcified cutting plates of holotype dissolved in preservative; maxillae weakly sclerotized (Fig. 2b). Maxillary formula: Mx I = 1 + 1; Mx II = 8 + 12; Mx III = 8 + 0; Mx IV = 7 + 9; Mx V = 1 + 1. Tube unknown.

Etymology. The new species is named in honour of the late Dr Hermann Augener who reported the first specimens.

Remarks. Although the only specimen is in a poor state of preservation, it is described as a new species since it can be clearly distinguished from its most closely related species *B. capense*, which is the only other known species of *Brevibrachium* with hooded tridentate spiny hooks. However, *B. capense* has hooks of varying sizes in the modified parapodia, while those of *B. augeneri* are of equal size. *Brevibrachium augeneri* differs further from *B. capense* in having only 4 instead of 5 modified pairs of parapodia, branchiae from setiger 2 with a maximum of 5 filaments (instead of from setiger 30–40 with single filaments throughout) and in the structure of the limbate setae.

Augener (1927) reported two small specimens from off southeast Australia as *Rhamphobranchium chuni*. Although the specimens have not been located, it is clear from his description and illustration of the tridentate spiny hook (Augener, 1927: fig. 8) that the two specimens are members of the new species. Augener considered the specimens juveniles of *R. chuni* and interpreted the tridentate nature of the spiny hooks as a juvenile character, a statement which has been repeated by Fauvel (1953). However, the present study

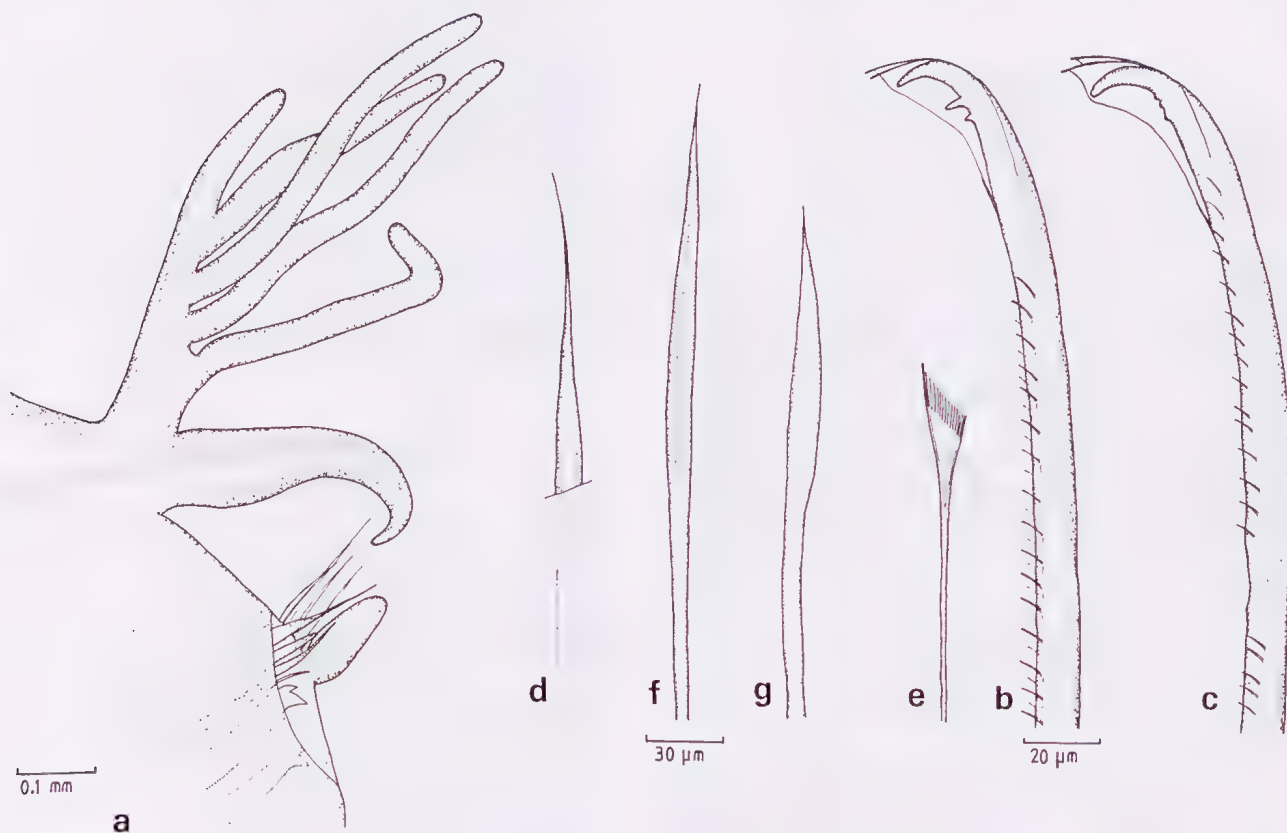


Fig. 1. *Brevibrachium augeneri* (holotype AM W.6268): a, parapodium 16, anterior view; b, simple spiny hook from setiger 1; c, pseudocompound spiny hook from setiger 3; d, aciculum from setiger 5; e, pectinate seta from setiger 9; f, upper limbate seta from setiger 5; g, lower limbate seta from same.

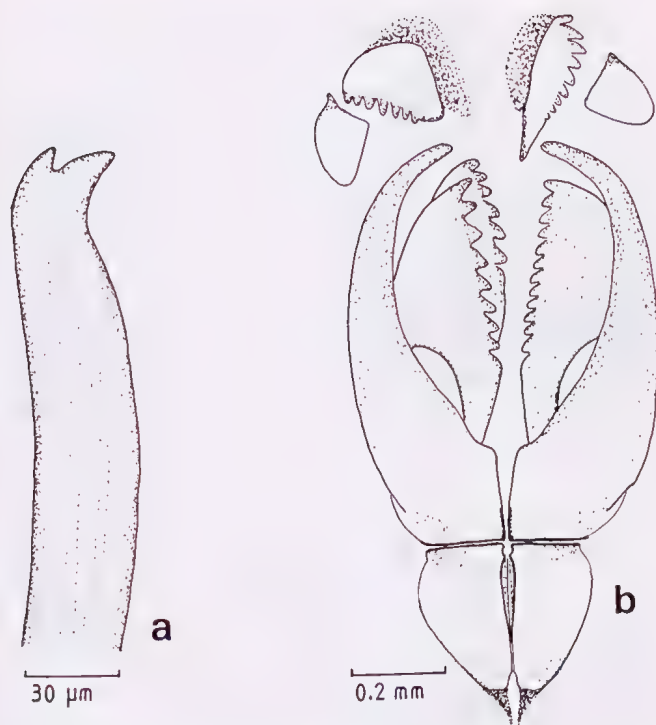


Fig. 2. *Brevibrachium augeneri* (holotype AM W.6268): a, subacicular hook from setiger 16; b, maxillae.

has proven this assumption to be incorrect, since *Rhamphobrachium* juveniles of much smaller size than the specimens examined by Augener have hooks with unidentate recurved distal ends, typical of the genus (Paxton, 1986).

Distribution. Pacific Ocean: southeast Australia; in 50–90 m.

Note. The two specimens reported by Augener (1972) as *Rhamphobrachium chuni* were located in the collections of the Zoological Museum, University of Copenhagen, while this paper was in press. It could be confirmed that the specimens are members of *B. augeneri* n. sp., as stated above.

Brevibrachium maculatum (Estcourt)

Fig. 3a–e

Rhamphobrachium maculatum Estcourt, 1966: 205, figs 1–3 (Three Kings Island, New Zealand, intertidal).—Knox & Hicks, 1973: 290, figs 33–43 (Coromandel and Kaikoura Peninsula, New Zealand); Day & Hutchings, 1979: 119 (previous records).

Rhamphobrachium chuni (not Ehlers, 1908).—Augener, 1924: 412 (Colville Channel, New Zealand).

Rhamphobrachium sp. Smith & Jensz, 1968: 777, fig. 1 (Victoria, Australia).

Material examined. Australia: Victoria: Aireys Inlet, Victoria, 23 Mar. 1968, R. L. Jensz & B. J. Smith, collectors—11 (NMV G1287–93). New Zealand: Auckland, rock pools, J. Whitley, collector—1 (USNM 33125).

Diagnosis. Anterior 3 pairs of parapodia modified; branchiae from setiger 15–17, single filament throughout; spineless, distally recurved hooks on

modified setigers; subacicular hooks from setiger 8–9.

Description. Length up to 42 mm, width up to 2 mm, number of setigers up to 107. Brownish pigmentation on prostomium, antennae, peristomium and anterior parapodia (Knox & Hicks, 1973: figs 33,34). Prostomium anteriorly rounded (Fig. 3a,b); posterior antennae on anterior part of prostomium, with ceratophores with 1–2 proximal rings and longer distal article, styles subulate to oval, reaching to setiger 1; small eyespots between bases of posterior and anterior lateral antennae; tentacular cirri subulate, far apart.

Anterior 3 pairs of parapodia modified, with rounded presetal lobes, truncate setal lobes and postsetal lobes with small accessory lobes (Fig. 3c). Following parapodia short, low presetal lobes, small round postsetal lobes, absent from setiger 8–10. Dorsal cirri subulate on modified parapodia, thereafter decreasing in size; ventral cirri subulate on anterior 3 setigers. Branchiae from setiger 15–17 as short processes, increasing rapidly in size, becoming strap-like, meeting in dorsal midline by setiger 20, shorter towards posterior region, absent on last 30 setigers.

Modified parapodia with 6–8 unidentate hooks of about equal size without hoods or spines (Fig. 3d), emerging in half-circle around setal lobe. All hooks simple, without any sign of fracture. Tips of acicula projecting slightly from parapodia 1–3, thereafter long and filiform. Bilimbate setae from parapodium 4, pectinate setae (comb with 20–25 teeth) in more posterior parapodia. Two hooded, bidentate subacicular hooks (Fig. 3e) from setiger 8–9.

Mandibles with slender shafts, calcified cutting plates dissolved in specimens examined; maxillae sclerotized (light brown in colour). Maxillary formula: Mx I = 1 + 1; Mx II = 5–7 + 5–6; Mx III = 4–6 + 0; Mx IV = 4–8 + 6–9; Mx V = 1 + 1. Tough, parchment-like tubes, often with right angle bends attached to holdfasts of algae (S. J. Whitley, collector), gastropod shells (Knox & Hicks, 1973), or lining burrows in hard limestone rock (Smith & Jensz, 1968).

Remarks. Knox & Hicks (1973) examined the holotype and gave a redescription of the species with which the specimens examined in this study agree well.

The two small specimens from Colville Channel, reported by Augener (1924) as juvenile *Rhamphobrachium chuni*, have not been found but were most likely *B. maculatum*. This decision is based on Augener's description of the dark pigmentation, and the origin and extent of branchiae. He mentioned that the hooks of the first three parapodia were 'characteristic' except for a weak pseudocompound fracture in the wrong direction. This fracture may have been an actual break in the hook. However, he did not state whether the hooks were spiny or not. Therefore, the record is considered uncertain.

Biology. This species lays spherical to ovoid eggs (0.3 to 0.5 mm diameter) in brood chambers partitioned off from the tube where the young undergo direct development. Sixteen young, ranging from 7 to 28

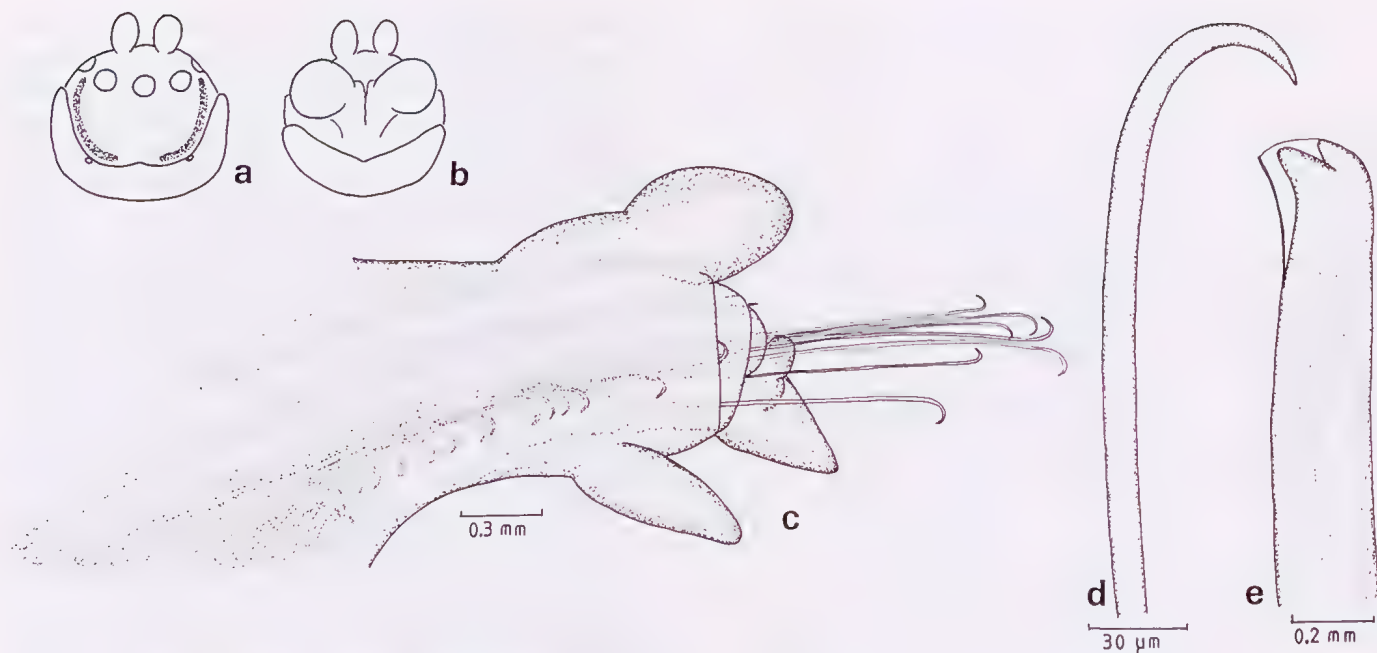


Fig. 3. *Brevibrachium maculatum* (NMV): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, parapodium I, anterior view; d, spineless hook from setiger 1; e, subacicular hook from setiger 12.

setigers, were taken from one tube, suggesting that egg-laying is staggered (Smith & Jensz, 1968).

Distribution. New Zealand (Three Kings Island, Kaikoura Peninsula and Auckland); Australia (Victoria); intertidal to 64 m.

Note. The two specimens reported by Augener (1924) as *Rhamphobrachium chuni* were located in the collections of the Zoological Museum, University of Copenhagen, while this paper was in press. The anterior hooks were found to be distally recurved and spineless, i.e. typical of *B. maculatum*.

Genus *Longibrachium* Paxton

Longibrachium Paxton, 1986: 43. Type species: *Rhamphobrachium atlanticum* Day, 1973: 55, by original designation. Gender: neuter.

Diagnosis. Anterior 4 pairs of parapodia prolonged, with more than 3 distally recurved hooks each; hooks with 2 rows of immoveable spines; setal sacs extending to setiger 20–60.

Remarks. For a full definition of the genus see Paxton (1986).

Key to Species of *Longibrachium*

1. Modified parapodia enormously prolonged, longer than body from setiger 1–20 (Fig. 4c); with 3 large and 4–10 small hooks; dorsal cirri of unmodified segments with basal processes (Fig. 4e). *L. longipes*
- Modified parapodia moderately to greatly prolonged, shorter than body from setiger 1–5; with large hooks only;

dorsal cirri of unmodified segments without basal processes. 2

2. Median antenna to setiger 13–15; hooks with long spines spaced far apart, continued to near end of hook. *L. atlanticum*
- Posterior antenna to setiger 6; hooks with short, closely spaced spines, absent from distal part of hook. *L. quadripes*

Longibrachium atlanticum (Day)

Rhamphobrachium atlanticum Day, 1973: 55, fig. 8a–h (North Carolina, U.S.A.; 19 m).—Gardiner, 1976: 195, fig. 25h,i (same record); Paxton, 1986: 43, fig. 26 a–e (definition of genus).

Material examined. U.S.A.: North Carolina: c. 34°34'N, 76°25'W, 19 m, 24 Jun. 1965—HOLOTYPE (USNM 43124) and PARATYPE (USNM 43125) and 1 (USNM 98878); Pierce sta. 1E, c. 33°12'N, 77°36'W, 44 m, 10 May 1977—1 (USNM 060925). Florida: Pierce sta. 7C, c. 29°31'N, 80°40'W, 18 m, 25 Nov. 1977—1 (USNM 061488).

Diagnosis. Median antenna longest, to setiger 13–15. Modified parapodia moderately prolonged; each with 4 large, spiny hooks; spines coarse, long, far apart, continued to near distal end of hook. Dorsal cirri on unmodified segments with basal swelling. Hooded subacicular hooks from setiger 20–25. Jaws without Mx VI.

Description. Length over 55 mm, segments over 85, width to 6 mm. Antennae and ventral surface of anterior parapodia with brown speckles (Paxton, 1986: fig. 26a). Ceratophores of antennae slender, with 4–5 proximal rings and longer distal ring; styles slender, anterior laterals to setiger 3(1–3), posterior laterals to 12(9–10), median posterior to 15(10–14). No eyes visible. Tentacular cirri long and slender, to distal end of frontal

palps; inserted close together, lying between median and posterior lateral antennae.

Modified parapodia moderately prolonged: parapodia 1–3 about equally long, extending slightly beyond prostomium when retracted; parapodia 4 shorter. Modified parapodia of all available specimens retracted; presetal, acicular and papilliform lobes not visible, postsetal lobes cirriform. Following parapodia short; low presetal lobes, conical postsetal lobes, reduced by setiger 25, continued posteriorly as small boss. Dorsal cirri long and stout on modified parapodia, thereafter shorter with basal swelling; ventral cirri conical on anterior 5 setigers. Small interramal papillae on setigers 7–12. Branchiae as single filaments from setiger 6, bifid from 8, maximum of 6–7 filaments from setiger 40–50.

Modified parapodia with 4 large, spiny hooks: spines coarse, long, far apart, continued to near distal end of hook. Setal sacs of hooks of parapodia 1–3 (holotype) extending in body cavity to setiger 60, hooks of parapodia 4 to setiger 40. Pectinate (comb with 15–20 teeth) and limbate setae from setiger 5. One hooded subacicular hook from setiger 31(20–25), 2 from 34(26–32), considerable variation with size of animal.

Mandibles weakly sclerotized; shafts long, cutting plates small and distally serrated (Paxton, 1986: fig. 26b). Maxillae brown (Paxton, 1986: fig. 26c); carriers rounded, maxillary formula: Mx I = 1 + 1; Mx II = 8 + 10; Mx III = 9 + 0; Mx IV = 8 + 10; Mx V = 1 + 1; Mx VI absent.

Remarks. The species was described by Day (1973) and Gardiner (1976) as having 3 pairs of modified anterior parapodia with spiny hooks. Examination of the types and other material shows that, although the fourth parapodia are shorter than the anterior 3, they are nevertheless modified, directed anteriorly (Paxton, 1986: fig. 26a) and bear spiny hooks.

Two types of tubes were in the vial together with the holotype. One tube consists of shell fragments, cemented together to form a smooth unlined inside. The other tube consists of a thin, parchment-like inner layer with sand grains attached on the outside. This type of tube is typical for members of the *Rhamphobranchium* complex and is considered as belonging to the holotype.

Biology. The three non-type specimens examined are much smaller than the two types. Their widths range from 1.1 to 3.0 mm. The smallest specimen (USNM 060925) is almost complete and measures 9.0 mm in length for 38 setigers. It has eyes at the bases of the posterior lateral antennae. Antennae are short; the longest, the median, reaches setiger 4. Only 3 pairs of parapodia are modified and bear spiny hooks, the fourth one has limbate setae like the following parapodia. Branchiae are present from setiger 6, as in adults, but reach only a maximum of 3 filaments. Bidentate subacicular hooks start on setiger 10.

Distribution. Western North Atlantic: U.S.A. (North Carolina and Florida); in 18–44 m.

Longibrachium longipes n. sp.

Figs 4a–e; 5a–k

Material examined. Australia: Queensland: Kimbla sta. Q11, off S end of Fraser Island, c. 25°48'S, 153°46'E, 73 m, 10 Nov. 1976, W. Ponder, R. Rowe, J. Lowry, collectors—HOLOTYPE (AM W.198973) and 2 PARATYPES (AM W.198974) and (USNM 98882).

Diagnosis. Median antenna longest, to setiger 9–12. Modified parapodia enormously prolonged; each with 3 large and 4–10 smaller spiny hooks; spines fine, short, closely set; continued to near distal end of hook. Dorsal cirri on unmodified segments with basal process. Subacicular hooks from setiger 26. Jaws with Mx VI.

Description. Length 34 + (17 + –20 +) mm, number of setigers 53 + (24 + –29 +), width 5.5(4.0–4.5) mm. Colour markings consisting only of light brown patches on middle part of posterior antennae. Prostomium short (Fig. 4a,b), ceratophores of antennae with 5–7 proximal rings and longer distal ring; anterior lateral styles to setiger 1, posterior laterals to 9 (7–8), median to ? (9–14). No eyes visible. Tentacular cirri to distal end of frontal palps; inserted close together, lying between median and posterior lateral antennae.

Modified parapodia enormously prolonged (Fig. 4c). When fully extended (as in USNM 98882) parapodia 1 about twice as long as medial posterior antenna, parapodia 2 and 3 progressively shorter, parapodia 4 shortest, about as long as posterior lateral antennae. In retracted state (as in holotype), parapodia only half as long and contracted into series of rings (Fig. 4d), becoming irregular at distal end. Modified parapodia with low acicular lobes, 3 papilliform lobes, digitiform postsetal lobes. Following parapodia short; low presetal lobes; conical postsetal lobes, reduced by setiger 25, continued posteriorly as small boss. Dorsal cirri digitiform with basal swelling developing into basal process by setiger 6 (Fig. 4e). Ventral cirri conical on 5 anterior setigers. Small interramal papillae on setigers 8–15. Branchiae as single filaments from setiger 7, bifid from 10(9–11), reaching maximum of 6 filaments by setiger 40.

Hooks of modified parapodia with short, closely spaced spines continued to near distal end. One thick, superior hook (Fig. 5a) projecting from each papilliform lobe, 4–10 thinner, shorter hooks (Fig. 5b) from lower fold. Setal sacs of hooks from parapodia 1–4 extending in body cavity to setigers 31, 27, 22, 17 respectively (in holotype). Limbate and pectinate setae from setiger 5 onwards; comb of anterior pectinate setae with 12 teeth (Fig. 5c), more posterior ones with 20–26 teeth (Fig. 5d). Anterior limbate setae with narrow wings; more posterior ones consisting of long unilimbate upper (Fig. 5e), shorter bilimbate median (Fig. 5f) and short (spine-like) bilimbate lower setae (Fig. 5g). One bidentate subacicular hook (Fig. 5h) from setiger 26, 2 from setiger 28.

Mandibles (Fig. 5i) white, strongly calcified; slender shafts and large cutting plates serrated at distal margin.

Maxillae (Fig. 5j) brown with whitish, calcified teeth; carriers oval, maxillary formula: Mx I = 1 + 1; Mx II = 7 + 8 (7 + 7); Mx III = 8 + 0 (7 + 0); Mx IV = 6 + 8 (5-6 + 7-8); Mx V = 1 + 1; Mx VI toothless plate. Tube unknown.

Etymology. The name *longipes* refers to the extremely prolonged anterior four pairs of parapodia which characterize this species.

Remarks. *Longibrachium longipes* differs mainly from its congeners by having two types of spiny hooks,

and dorsal cirri with basal processes.

Biology. In one paratype (AMS W.198974) some of the anterior parapodia are partly regenerated. One parapodium of setiger 2 is very short. Incomplete internal hooks are of the normal type, but the protruding 3 hooks are very thin, with few spines, and are bidentate and hooded (Fig. 5k).

Distribution. South Pacific: Australia (Queensland); in 73 m.

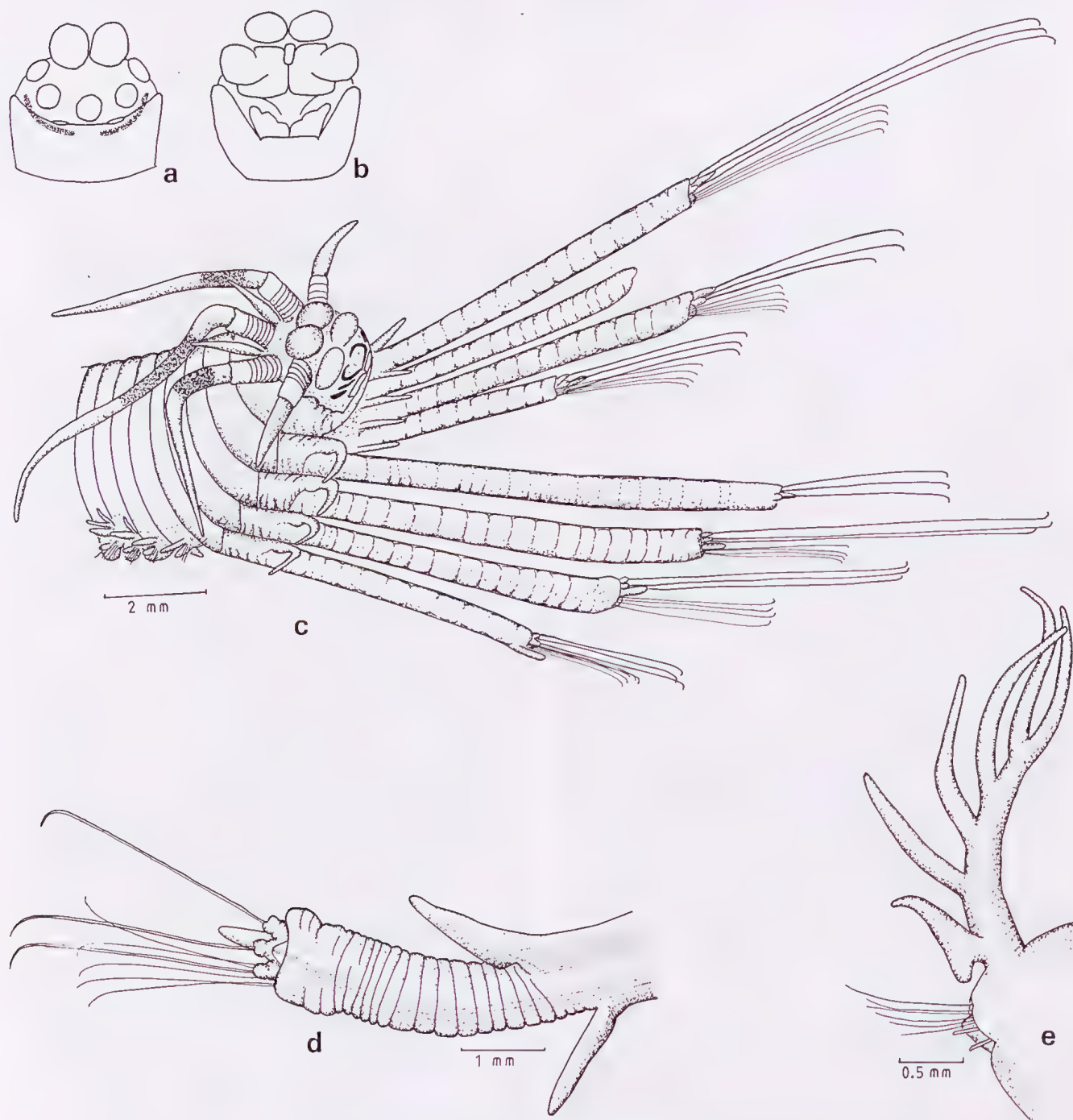


Fig. 4. *Longibrachium longipes* (c: paratype 1 USNM; d,e: holotype AM W.198973): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, anterior end, dorsolateral view; d, parapodium 3, anterior view; e, parapodium 45, anterior view.

Longibrachium quadripes (Kucheruk)

Rhamphobrachium quadripes Kucheruk, 1979a: 1229, fig. 3 (Gulf of Tonkin, 157 m).

Diagnosis. Posterior antennae equally long, to setiger 6. Modified parapodia greatly prolonged; each with large spiny hooks; spines fine, short, closely spaced;

absent from distal part of hook. Dorsal cirri on unmodified segments with basal swelling. Hooded subacicular hooks from setiger 16. Jaws unknown.

Description. Length over 15 mm, setigers over 31, width 4.5 mm. Ceratophores of antennae with 6 rings; styles short, posterior median and laterals to setiger 6. Digitiform tentacular cirri.

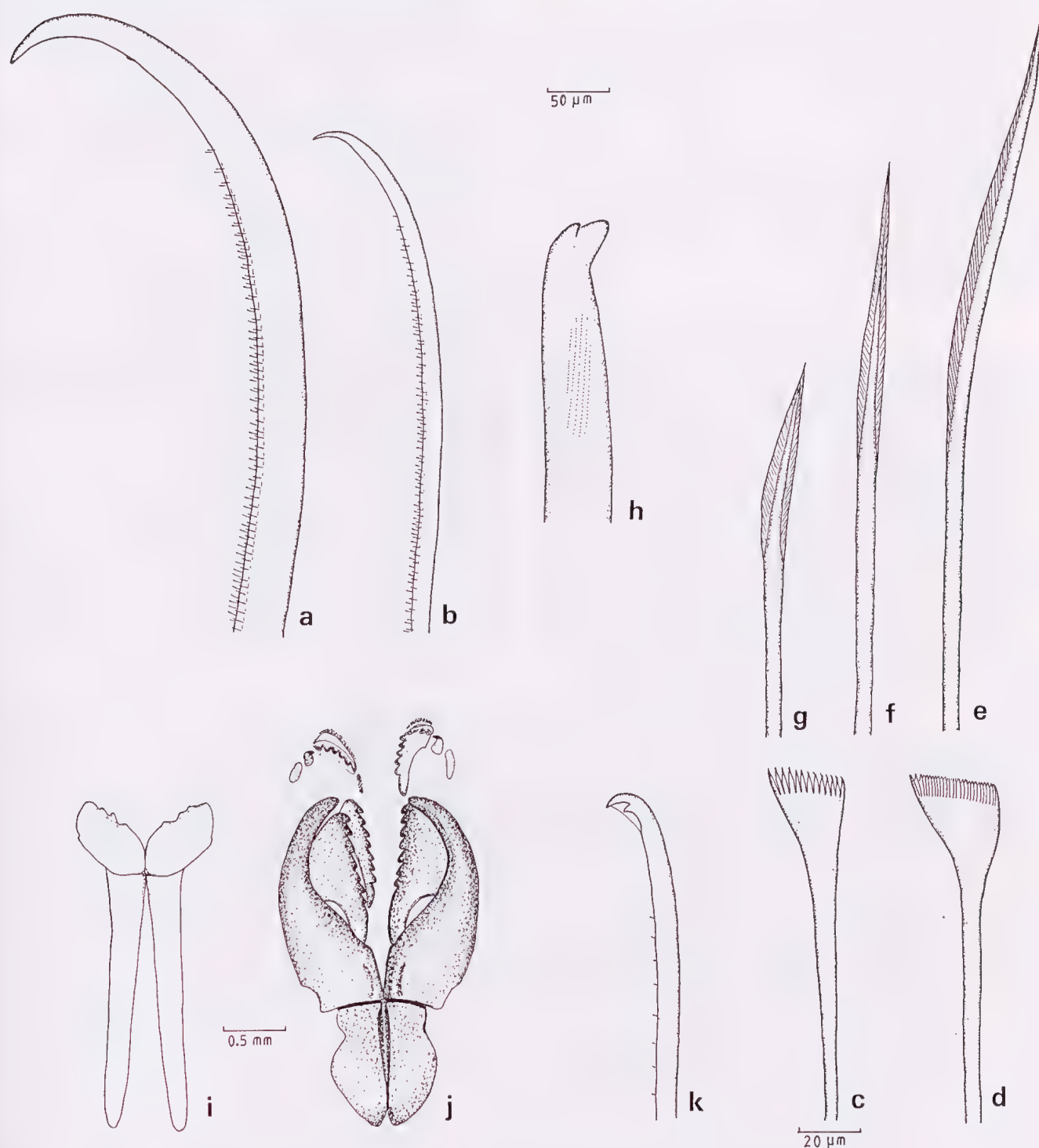


Fig. 5. *Longibrachium longipes* (a,b,h: holotype AM W.198973; d-g: paratype 1 USNM 98882; c, i-k: paratype AM W.198974); a, large spiny hook from setiger 2; b, small spiny hook from same; c, pectinate seta from setiger 5; d, pectinate seta from setiger 28; e, upper unilimbate seta from setiger 26; f, median bilimbate seta from setiger 26; g, lower spine-like limbate seta from setiger 26; h, subacicular hook from setiger 44; i, mandibles; j, maxillae; k, bidentate spiny hook from regenerating parapodium 2.

Modified parapodia greatly prolonged, with short postsetal lobes. Following parapodia short; digitiform postsetal lobes, absent from setiger 15–16. Dorsal cirri with basal swelling, ventral cirri on 5 anterior parapodia. Single branchial filaments from setiger 8, bifid from 13, maximum of 5 filaments on setigers 20–22, decreasing thereafter.

Hooks of modified parapodia with small, closely spaced spines, distal portion spineless; setal sacs of hooks from parapodia 1–3 to setiger 20, parapodia 4 to setiger 12. Limbate and pectinate setae (comb with 20 teeth) from setiger 5. Hooded bidentate subacicular hooks from setiger 16.

Jaws 'typical for the family' (Kucheruk, 1979).

Remarks. The single specimen on which the original description was based was not available for examination.

Distribution. Western North Pacific Ocean: Gulf of Tonkin; in 157 m.

Genus *Rhamphobrachium* Ehlers

Rhamphobrachium Ehlers, 1887: 70. Type species: *Rhamphobrachium Agassizii* Ehlers, 1887: 70, by subsequent designation of Hartman, 1944: 47. Gender: neuter.

Paranorthia Moore, 1903: 448. Type species: *Paranorthia brevicornuta* Moore, 1903: 448, by monotypy and subsequent designation of Hartman, 1959: 306.

Diagnosis. Anterior 3 pairs of parapodia prolonged, with 3 distally recurved hooks each; hooks with 2 rows of moveable spines, setal sacs extending to setiger 30–60.

Remarks. For a full definition of the genus see Paxton (1986).

Two species of *Rhamphobrachium*, *R. agassizii* Ehlers, 1887 (type species) and *R. chuni* Ehlers, 1908, differ in a number of characters from the remaining species. These differences are here considered to be of sufficient status to warrant the division of the genus into two subgenera.

Rhamphobrachium agassizii and *R. chuni* are referred to the nominal subgenus which is characterized by: all limbate setae simple; subacicular hooks reaching a maximum number of 3–6 per parapodium on setigers 15–30; maxilla VI present. The remaining species are referred to the new subgenus, *Rhamphobrachium (Spinigerium)* (type species *R. longisetosum* Berkeley & Berkeley, 1938) which is characterized as follows: lower limbate setae pseudocompound to compound; number of subacicular hooks per parapodium not exceeding 2; maxilla VI absent.

Prior to the present study, five species were described based on specimens with only two pairs of modified parapodia. The elucidation of *Rhamphobrachium* development (Paxton, 1986) has shown that specimens with two pairs of modified parapodia are juveniles. For one of these, *R. averincevi* Kucheruk, 1979, the availability of a large size range of specimens from near the type locality, spanning from juveniles to adults, made it possible to emend the definition of the species to its adult features.

Rhamphobrachium golikovi Averincev, 1972 and *R. sp.* Averincev, 1972 are considered as juveniles of *R.(S.) ehlersi* and are here referred to this species.

Rhamphobrachium (S.) bipes Monro, 1937, *R.(S.) brevicornutum* (Moore, 1903), and *R.(S.) cristobalensis* Fauchald, 1968 are juveniles that cannot be aligned with any known species at the present time and are treated as *incertae sedis*.

Key to Species of *Rhamphobrachium*

1. Tentacular cirri inserted far apart (Fig. 7a); lower limbate setae pseudocompound (Fig. 7d,e) to compound (= spinigers) (Fig. 12g-i); maximum of 2 subacicular hooks per parapodium; Mx VI absent (Fig. 8h).
..... *R. (Spinigerium)*...3
- Tentacular cirri inserted close together (Fig. 6a); all limbate setae simple; maximum of 3–6 subacicular hooks on setigers 15–30 (Fig. 6d); Mx VI present (Fig. 6f).
..... *R. (Rhamphobrachium)*...2
2. Branchiae from setiger 16–17; early unmodified parapodia with well developed, subulate postsetal lobes; recurved hooks weakly pseudocompound.
..... *R.(R.) agassizii*
- Branchiae from setiger 12–14; early unmodified parapodia with short postsetal lobes (Fig. 6c); recurved hooks simple. *R.(R.) chuni*
3. Lower limbate setae compound; falcigers (Fig. 9d) present or absent on setigers 4 and 5. 9
- Lower limbate setae pseudocompound (Fig. 7d,e); falcigers absent. 4
4. Branchiae with maximally 1 or 2 filaments. 5
- Branchiae with 4 or more filaments. 7

5. Branchiae with 1 filament only; subacicular hooks from setiger 10–11.
..... *R.(S.) pettiboneae*
——Branchiae with maximally 2 filaments; subacicular hooks from setiger 12–16.
..... 6
6. Branchiae from setiger 14; posterior antennae with 4–5 rings, reaching to
setiger 3–6. *R.(S.) pyriforme*
——Branchiae from setiger 10–12; posterior antennae with 2–3 rings, reaching
to setiger 1–2. *R.(S.) ehlersi*
7. Branchiae from setiger 11–14. *R.(S.) verngreni*
——Branchiae from setiger 6–9. 8
8. Branchiae from setiger 6–8, maximally 4 filaments; subacicular hooks from
setiger 16–18. *R.(S.) averincevi*
——Branchiae from setiger 8–9, maximally 8–10 filaments; subacicular hooks
from setiger 12–14. *R.(S.) longisetosum*
9. Branchiae from setiger 10, maximally 8 filaments. *R.(S.) diversosetosum*
——Branchiae from setiger 11–13, maximally 4–6 filaments. 10
10. Antennae on anterior part of prostomium (Fig. 13a); postsetal lobes of
modified parapodia short and rounded (Fig. 13c). *R.(S.) noeli*
——Antennae on median part of prostomium (Fig. 12a); postsetal lobes of
modified parapodia longer and subulate (Fig. 12b). 11
11. Falcigers (Fig. 12f) on setigers 4 and 5. *R.(S.) hutchingsae*
——Falcigers on setiger 4 only, or absent. *R.(S.) brevibrachiatum*

Subgenus *Rhamphobranchium*

Diagnosis. All limbate setae simple.

Definition. Posterior antennae on median part of prostomium (Fig. 6a). Labial palps with distinct anterior median section (Fig. 6b). Nuchal grooves with small middorsal separation. Tentacular cirri subulate, inserted distally on peristomium, very long, to near distal end of frontal palps; inserted close together, lying between median and posterior lateral antennae. Branchiae from setiger 12–16, pectinate filaments. Recurved hooks simple to weakly pseudocompound. Lower limbate setae simple; falcigers absent; 1–2 subacicular hooks per parapodium from setiger 13–15, maximum of 3–6 from 15–30 (Fig. 6d), thereafter 2. Maxilla VI present.

Size. Large; length to 19+ cm (190+ setigers), width to 7 mm.

Distribution. North Atlantic, Indian and Pacific Oceans; 764 to 2165 m.

Rhamphobranchium (Rhamphobranchium) agassizii Ehlers

Rhamphobranchium Agassizii Ehlers, 1887: 70, pl. 17 figs 1–5, pl. 18 figs 1–9 (in part) (Carysfort Reef, Florida, U.S.A., 642 m).—Fauvel, 1914: 126 (Azores and Morocco); Treadwell, 1939: 258, fig. 76 (Puerto Rico); [?] Intes & Le

Loeuff, 1975: 312 (Ivory Coast); Paxton, 1986: 44, fig. 27 (definition of genus).

Material examined. U.S.A.: Florida: *Blake*, off Carysfort Reef, 642 m, 23 Mar. 1869—LECTOTYPE designated herein (MCZ 789). **Puerto Rico:** Johnson-Smithsonian Expedition sta. 67-354E, 18°32'18"N, 65°46'12"W, 549–599 m, 23 Feb. 1933–3 (USNM 20070).

Diagnosis. Early unmodified parapodia with well developed triangular postsetal lobes; branchiae from setiger 16–17. Recurved hooks weakly pseudocompound.

Description. Length 22+ (to 37+) mm, setigers 29+ (to 49+), width 4 (to 4) mm. Prostomium anteriorly rounded (Paxton, 1986: fig. 27a,b). Ceratophores of antennae with 2–3 proximal rings and longer distal ring; anterior lateral styles to setiger 1, posterior laterals to 4 (3), median to 3 (2).

Each of parapodia 1–3 with 3 short papilliform lobes and one longer subulate postsetal lobe. On setiger 4 (Paxton, 1986: fig. 27c) low presetal and triangular postsetal lobes, latter decreasing in size and absent from setiger 10. Dorsal cirri digitiform, long on anterior 3 setigers, shorter on 4 and 5, remaining constant from 6 onwards. Single branchial filaments from setiger 17(16–17), bifid from 18–21, reaching maximum of 5 filaments by setiger 30.

Modified parapodia with weakly pseudocompound, long, recurved hooks (Paxton, 1986: fig. 27d,e), setal

sacs to setiger 55. Pectinate setae (comb with 12–25 teeth) and limbate setae from setiger 4; latter longest (Paxton, 1986: fig. 27f) in upper position, shorter in median, and short spine-like in lower position. One to 2 subacicular hooks per parapodium from setiger 15(14–15), maximum of 3–5 from 16(15–20) (Paxton, 1986: fig. 27i,j), 2 from 20(20–21) to presumably end of body.

Jaws (Paxton, 1986: fig. 27k,l) strongly calcified; mandibular shafts slender, cutting plates distally serrated. Maxillae weakly sclerotized, light brown; maxillary formula: Mx I = 1 + 1; Mx II = 8 + 8 (8–9); Mx III = 7 (6–7) + 0; Mx IV = 6 + 8 (7–9); Mx V = 1 + 1; Mx VI toothless plate. Tubes with parchment-like inner layer and outer layer of mud and sand.

Remarks. Ehlers (1887) described *R. agassizii* on the basis of five specimens collected in four different stations; all were taken by the U.S. Coast Survey Steamer *Blake* in the Caribbean, at depths exceeding 600 m. The five syntypes were examined in the present study, and only one (MCZ 789), the largest specimen, agreed with the description and illustrations, while the other four specimens were found to belong to another species, *R. (S.) brevibrachiatum* (see ‘Remarks’ for *R. brevibrachiatum*). Thus the only type specimen of *R. (R.) agassizii* (MCZ 789) that matches Ehlers’ description is herewith designated the lectotype.

The lectotype consists of 29 setigers, not 20 as stated by Ehlers. Although it is not in the best condition (it was dried up at some stage and some of the setae have crystalline deposits), it can be clearly identified with Ehlers’ drawings.

The three specimens from Puerto Rico (USNM 20070) are smaller, measuring from 2.6–3.0 mm in width. The setae of these specimens vary in two aspects from those of the lectotype: (1) the comb of the pectinate setae has 12–20 teeth in the lectotype and 18–25 in the specimens from Puerto Rico; and (2) the maximum number of subacicular hooks is 3 (Paxton, 1986: fig. 27i) in the former and 4–5 (Paxton, 1986: fig. 27j) in the latter. Since there is agreement in all other aspects, the specimens from Puerto Rico are considered members of *R. (R.) agassizii* and the variation may be ascribed to their smaller size.

Ehlers described the tubes as consisting of an inner parchment layer, covered on the outside with foraminiferans and other fragments. However, these tubes belong to the specimens of *R. (S.) brevibrachiatum*. The tube of the lectotype of *R. (R.) agassizii* consists of an inner parchment-like layer covered on its outside with a mud and sand layer. The specimens from Puerto Rico have similar tubes, but a thicker outer layer.

Biology. The lectotype is a male specimen, containing sperm morulae and free sperm.

Distribution. Eastern North Atlantic: U.S.A. (Florida) and Puerto Rico; western North Atlantic: Azores, Morocco and Ivory Coast; ?40–2165 m.

Rhamphobrachium (Rhamphobrachium) chuni Ehlers Fig. 6a–f

Rhamphobrachium chuni Ehlers, 1908: 76, pl. 9 figs 6–15 (Nias Canal, Indonesia, 677 m and East Africa, 1362 m).—Fauvel, 1932: 150 (Indian Ocean); 1953: 261, fig. 132a,b (same record); [?] Day, 1967: 420 (Natal); [?] Knox & Hicks, 1973: 293, figs 44,45 (New Zealand); [?] Stull, 1979: 32 (New Zealand).

Rhamphobrachium pacifica Hoagland, 1920: 618, pl. 49 figs 15–23 (Basa Island, Philippines, 703 m).

Material examined. **Indonesia:** *Valdivia* sta. 198, Nias Canal, c. 0°16'N, 98°07'E, 677 m—SYNTYPE (ZMH PE-759). **East Africa:** *Valdivia* sta. 258, c. 2°58'N, 46°50'E, 1362 m, 28 Mar. 1899—SYNTYPE (ZMB 4446). **Philippines:** *Albatross* sta. 5656, Olang Point, Basa Island, 703 m, 19 Dec. 1909—HOLOTYPE of *R. pacificum* (USNM 18959); *Albatross* sta. 5348, Point Tabonan, Palawan Passage, 686 m, 27 Dec. 1908—1 (USNM 18999).

Diagnosis. Early unmodified parapodia with short postsetal lobes; branchiae from setiger 12–14. Recurved hooks simple.

Description. Length 19+ (to 42+) cm, setigers 190+ (to 87+), width 4.5 (to 7.0) mm. Prostomium anteriorly rounded (Fig. 6a,b). Ceratophores of antennae with 2–4 proximal rings and longer distal ring; anterior lateral styles to setiger 1, posterior laterals to 3, median to 2.

Each of parapodia 1–3 with 3 short papilliform lobes and one longer subulate postsetal lobe. On setiger 4 (Fig. 6c), low presetal and short postsetal lobes, latter absent from setiger 10. Dorsal cirri subulate, long on anterior 3 pairs of parapodia, shorter on setiger 4 and 5, remaining constant from 6. Single branchial filaments from setiger 12–14, bifid from 15–16, maximum of 6 filaments from setiger 30–40, thereafter decreasing and absent from setiger 145.

Modified parapodia with simple long recurved hooks, setal sacs to setiger 55. Pectinate setae (comb with 15–20 teeth) and limbate setae from setiger 4; latter weakly uni- to bilimbate, longest in upper, shortest in lower position. One to 2 subacicular hooks per parapodium from setiger 16(13–15), maximum of 5–6 (Fig. 6d) from 17(16–20), 3–4 from 20(18–30), 2 from 23(25–30) to end of body (variation with size of animal).

Jaws strongly calcified, mandibular shafts slender, cutting plates distally smooth (Fig. 6e). Maxillae weakly sclerotized, light brown; maxillary formula: Mx I = 1 + 1; Mx II = 7 (10) + 9 (9); Mx III = 8 (6) + 0; Mx IV = 6 (7) + 8 (7); Mx V = 1 + 1; Mx VI toothless plate (Fig. 6f). Tubes with parchment-like inner layer and thick outer layer of black mud (Ehlers, 1908).

Remarks. Ehlers (1908) stated that the setal bundle contained two or three subacicular hooks. He overlooked the number of subacicular hooks in more anterior segments which reaches a maximum of five or six.

Hoagland (1920) described *R. pacificum* from the Philippines. Apparently she was not aware of *R. chuni*, since she compared her specimens to *R. agassizii* but

not *R. chuni*. The holotype of *R. pacificum* was examined and found to agree with *R. chuni*; thus the former name is a junior synonym of the latter.

The branchiae do not start on the eleventh parapodium as stated by Hoagland, but on setiger 13 (USNM 18959) and setiger 14 (USNM 18999). Although the branchial filaments are infrequently subdivided, I have not found another parapodium where the dorsal cirrus is bifid as shown by Hoagland (1920: pl.49 fig. 19) and consider it as abnormal growth.

Distribution. Indo-Pacific: East Africa, India, Indonesia, Philippines, ?New Zealand; ?64 to 1362 m.

Rhamphobrachium (*Rhamphobrachium*) sp.

Material examined. Australia: Victoria: *Esso-Gipps* sta. 19, Bass Strait, c. 39°S, 148°30'E, 126 m, 7–9 May 1969—2 (AM W.198964); *Esso-Gipps* sta. 20, 110 km S of Lakes Entrance, c. 39°S, 148°24'50"E, 95 m, May 1969, C. Phipps, collector—4 (AM W.198965). New South Wales: Palm Beach, Sydney, 33°35'03"S, 151°21'30"E, 31 m, 10 Dec. 1977, F. Talbot *et al.*, collectors—16 (AM W.198966); same locality and collectors, 17 Mar. 1978—7 (AM W.198967).

Remarks. The samples consist of young juveniles, lacking frontal palps, tentacular cirri and branchiae [see Paxton (1986) for description]. The absence of pseudocompound or compound limbate setae marks them as members of the subgenus *Rhamphobrachium*, but specific identification is not possible.

Distribution. Pacific Ocean: southeast Australia; 31–126 m.

Spinigerium n. subgen.

Type species: *Rhamphobrachium longisetosum* Berkeley & Berkeley, 1938: 428. Gender: neuter.

Diagnosis. Lower limbate setae pseudocompound to compound (= spinigers).

Definition. Posterior antennae on anterior (Fig. 13a) to median part of prostomium (Fig. 12a). Labial palps with indistinct anterior median section (Fig. 7b). Nuchal grooves with large middorsal separation. Tentacular cirri subulate, inserted distally to subdistally on peristomium, moderately long to long, rarely reaching frontal palps; inserted far apart, lying between anterior and posterior lateral antennae. Branchiae from setiger 6–13, single or pectinate filaments. Recurved hooks pseudocompound (Fig. 14d). Lower limbate setae pseudocompound (Fig. 7d,e) to compound (= spinigers) (Fig. 12g–i); falcigers (Fig. 9d) sometimes present; subacicular hooks (Fig. 8g) from setiger 10–16, maximum of 2 per parapodium. Maxilla VI absent.

Size. Small to moderately large; length to 57+ mm for 73+ setigers; width to 5 mm.

Etymology. The name refers to the presence of spinigers in the early unmodified parapodia.

Distribution. World-wide; intertidal to 1470 m.

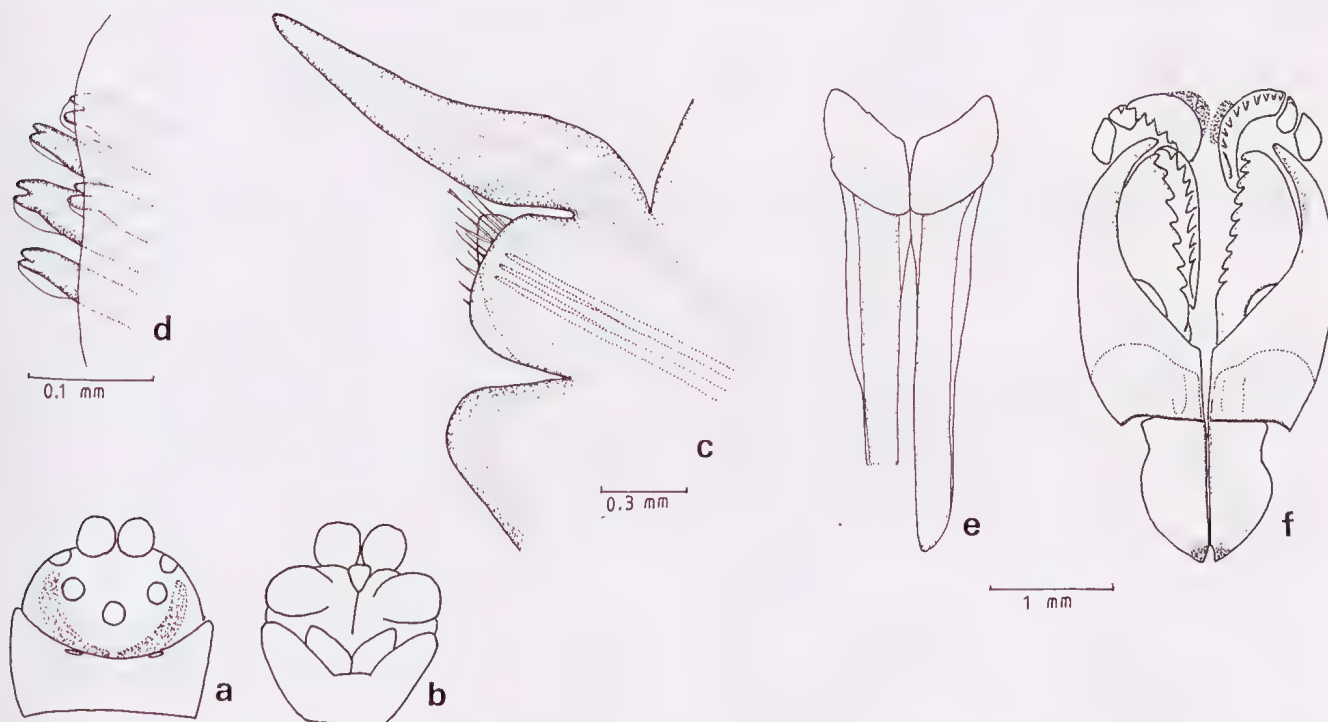


Fig. 6. *R. (Rhamphobrachium) chuni* (c,d: syntype ZMB 4446; e,f: syntype ZMH PE-759): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, parapodium 4, anterior view; d, subacicular hooks from setiger 17; e, mandibles; f, maxillae.

Rhamphobrachium (Spinigerium) longisetosum

Berkeley & Berkeley

Fig. 7a-g

Rhamphobrachium longisetosum Berkeley & Berkeley, 1938: 428, figs 1-8 (Southern California, U.S.A., 31 m).—Hartman, 1944: 48, pl. 1 figs 1-8 (Southern California, Mexico, Galapagos Islands); 1968: 705, figs 1-5 (same records); Pettibone, 1967: 8 (list of Berkeley types); Fauchald, 1968: 46 (Mexico).

Material examined. U.S.A.: California: off mouth of Santa Ana River, 31 m, G.E. MacGinitie, collector—SYNTYPE (USNM 32865); off Balboa, 60 m, 19 May 1933, G.E. MacGinitie, collector—SYNTYPE (USNM 32866); *Velero* sta. 890-38, 908-39, 1012-39, 1018-39, 1023-39, 1125-40, 1130-40, 1131-40, 1149-40, southern California, 45-275 m (for detailed station data see Hartman, 1944)—15 (AHF).

Diagnosis. Posterior antennae on median part of prostomium; branchiae from setiger 8-9, reaching maximum of 8-10 filaments by setiger 35; setigers 1-4 with moderately long postsetal lobes; one subacicular hook from setiger 12-14, 2 from 15-17.

Description. Length 8+ (to 34+) mm, setigers 9+ (to 47+), width 5 (to 5) mm. Pigmentation, often bleached by preservatives, consisting of longitudinal pale brown band on prostomium and spots on ceratophores and dorsal surface of anterior segments. Posterior antennae on median part of prostomium (Fig.

7a,b). Ceratophores of antennae with 4 (3-6) proximal rings and longer distal ring; styles subulate, anterior lateral styles to setiger 2(1-2), posterior laterals to 5(3-5), median to 4(4). Small eyespots between lateral antennae (bleached out in most specimens examined). Tentacular cirri long, almost reaching frontal palps.

Each of parapodia 1-3 with 3 short papilliform lobes and one longer subulate postsetal lobe. On setiger 4 (Fig. 7c), low presetal and moderately long subulate postsetal lobes, latter reduced from setiger 5 and absent from 15-20. Dorsal cirri subulate. Single branchial filaments from setiger 8-9, bifid from 15-17, maximum of 8-10 filaments by setiger 35.

Modified parapodia with long recurved hooks, setal sacs to about setiger 50. From setiger 4, pectinate (comb with 12-20 teeth) and simple long upper limbate setae projecting from dorsal pocket. Lower bundle with pseudocompound median and lower limbate setae (Fig. 7d), becoming gradually shorter, cultriform (Fig. 7e) and spine-like bilimbate (Fig. 7f) in following parapodia. One bidentate hooded subacicular hook from setiger 12-14, 2 from 15-17.

Calcified cutting plates of mandibles (Fig. 7g) with tooth-like projection near point of fusion. Maxillary formula: Mx I = 1 + 1; Mx II = 6-7 + 7; Mx III = 7-8 + 0; Mx IV = 7-8 + 9-11; Mx V = 1 + 1 (large plate). Tubes with tough parchment-like inner layer and outer sandy layer.

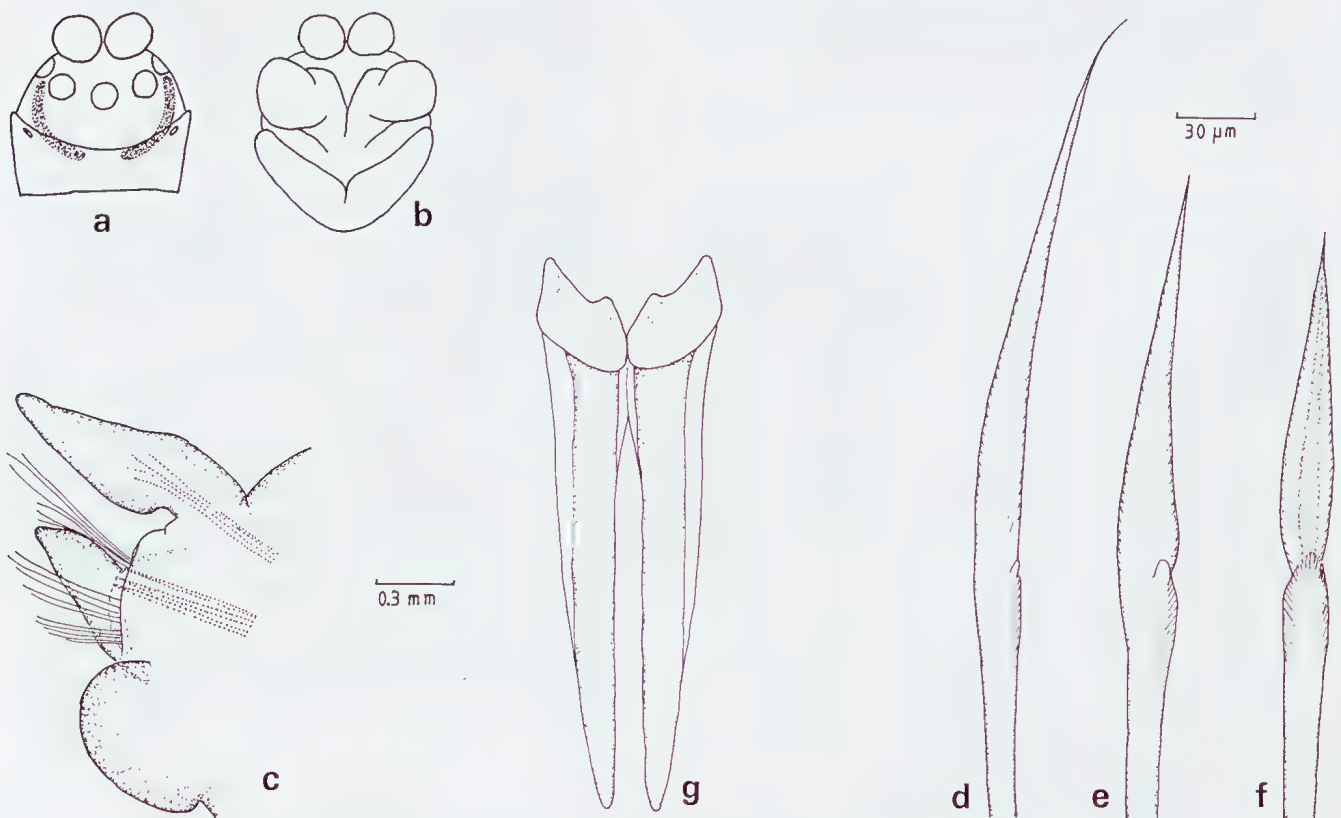


Fig. 7. *R. (Spinigerium) longisetosum* (c-f: AHF *Velero* sta. 1131-40; g: AHF *Velero* sta. 890-38): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, parapodium 4, anterior view; d, pseudocompound lower limbate seta from setiger 4; e, pseudocompound cultriform limbate seta from setiger 19; f, pseudocompound spine-like limbate seta from same; g, mandibles.

Distribution. Pacific Ocean: U.S.A. (Southern California to Mexico); Galapagos Islands; 20–730 m.

Rhamphobrachium (Spinigerium) averincevi Kucheruk
Fig. 8a–h

Rhamphobrachium chuni (not Ehlers, 1908).—Knox, 1960: 126 (Chathams, S of New Zealand).

Rhamphobrachium averincevi Kucheruk, 1979b: 120, figs 1–10 (S of New Zealand, 1200–1400 m).

Material examined. New Zealand: sta. MU68-29, Karitane Canyon, 580 m, S. Rainer, collector—1 (PML); sta. MU73-186, Papanui Canyon, c. 45°52'S, 171°01'E, 480 m, sandy mud, 24 Aug. 1973, P.K. Probert, collector—1 (PML); sta. MU74-92, Papanui Canyon, c. 45°51'S, 171°01'E, 420–320 m, muddy sandy gravel, 24 Mar. 1974, P.K. Probert, collector—1 (PML); sta. Q723, off South Island west coast, c. 41°58.5'S, 170°28.1'E, 507 m, muddy sand, 4 Mar. 1982, P.K. Probert, collector—1 (NZOI); sta. Q727, off South Island west coast, c. 40°58.5'S, 171°40.9'E, 134 m, muddy sand, 5 Mar. 1982, P.K. Probert, collector—3 (NZOI); sta. Q729, off South Island west coast, c. 40°51.8'S, 171°28.0'E, 195 m, sand 6 Mar. 1983, P.K. Probert, collector—3 (NZOI); *Eltanin* sta. 1989, c. 53°29' to 53°30'S, 169°48' to 169°45'E, 589–594, 1 Jan. 1968—1 (USNM).

Diagnosis. Posterior antennae on median part of prostomium; branchiae from setiger 6–8, maximum of 3–6 filaments by setiger 35–40; setigers 1–4 with moderately long postsetal lobes; one subacicular hook from setiger 15–18, 2 from 17–20.

Description. Length to 25+ mm, number of setigers to 42+, width to 4 mm. Prostomium and anterior parapodia with light brown patches of pigment. Posterior antennae on median part of prostomium. Ceratophores of lateral antennae with 3–4, median antenna with 2–3 proximal rings and long distal ring. Styles subulate; anterior laterals to setiger 1–2, posterior laterals to 3–5, median to 2–4. Small eyespots between anterior and posterior lateral antennae. Tentacular cirri subulate, longer than ceratophores, reaching to bases of frontal palps.

Each of parapodia 1–3 (Fig. 8a) with 3 short papilliform lobes and one longer subulate postsetal lobe. On setiger 4 (Fig. 8b), low presetal and moderately long subulate postsetal lobes, latter reduced from setiger 5 and absent from 20–25. Dorsal cirri subulate, ventral cirri subulate on setigers 1–3, oval on setiger 4. Single branchial filaments from setiger 6–8, bifid from 16–19, reaching maximum of 3–6 filaments by setiger 35–40 (Fig. 8c).

Modified parapodia with long recurved hooks, setal sacs to about setiger 60. From setiger 4, pectinate (comb with 10–20 teeth) and simple long upper limbate setae projecting from dorsal pocket. Lower bundle with weakly pseudocompound median and lower (Fig. 8d) limbate setae, becoming shorter, cultriform (Fig. 8e) and bilimbate spine-like (Fig. 8f) in following setigers. One subacicular hook (Fig. 8g) from setiger 15–18, 2 from 17–20.

Calcified cutting plates of mandibles partly dissolved. Maxillae (Fig. 8h) weakly sclerotized; maxillary formula: Mx I = 1 + 1; Mx II = 7 + 9; Mx III = 7 + 0; Mx IV = 5 + 9; Mx V = 1 + 1 (large plate). Tubes with parchment-like inner layer and outer layer of foreign particles.

Remarks. *Rhamphobrachium (S.) averincevi* was described by Kucheruk (1979b) on the basis of two specimens, collected south of New Zealand in 1200–1400 m. He characterized the species as having 2 pairs of modified parapodia with recurved hooks, parapodia 3 with compound limbate setae and falcigers, and single branchial filaments from setiger 13–27. The presence of only two pairs of modified parapodia marks the type specimens as juveniles.

The specimens examined during the present study were of a wide size range, ranging in width from 0.5–4.0 mm and belonging to stages 1, 2, 4 and adults [as defined for *R.(S.) ehlersi*, see Paxton (1986)]. Single branchial filaments are present from setiger 10–13 in juveniles, 8–10 in young adults, and 6–8 in adults. Since the juvenile specimens agree with the description of *R.(S.) averincevi* and are from the vicinity of the type locality, it appears certain that the specimens are conspecific. The original description of *R. (S.) averincevi* is here emended to the adult features of the species.

Knox (1960) reported *R. chuni* from the Chatham Islands. He stated that the branchiae commenced on the 6th setiger. Since *R.(S.) averincevi* is the only species with branchiae from setiger 6 in adults, and occurs near the collecting area, the record is here referred to *R.(S.) averincevi*.

Distribution. South Pacific Ocean: South of New Zealand; 134–1400 m.

Rhamphobrachium (Spinigerium) brevibrachiatum
(Ehlers)
Fig. 9a–g

Diopatra brevibrachiata Ehlers, 1875: 49, pl. 3 figs 11–21 (W of English Channel, 1247 m).

Rhamphobrachium brevibrachiatum.—Ehlers, 1887: 72 (new combination); Bellan, 1964: 89, figs 5–7 (Mediterranean); Amoureux, 1972: 75 (Spain); 1974: 136 (Portugal); 1977: 398 (English Channel).

Rhamphobrachium agassizii (not Ehlers, 1887).—Ehlers, 1887: 70 (in part) (Florida); [?] Hartman, 1965: 113 (NE South America).

Onuphis (Diopatra) brevibrachiata.—McIntosh, 1903: 133, pl. 10 figs 5–10 (Strait of Gibraltar; E of Cape de Gatte).

Onuphis brevibrachiata.—McIntosh, 1910: 407, pl. 63 figs 8, 8a, 10, 10a; pl. 75 figs 6, 6a; pl. 84 figs 4–4c (previous records); Fauvel, 1923: 417, fig. 165a–e (previous records).

Material examined. Spain: *Porcupine*, E of Strait of Gibraltar, probably 35°39' to 37°25'N, 1°56' to 1°10'W, 655 m, 1870—1 (BMNH ZK 1921.5.1.1695). U.S.A.: Virginia: *Iselin* sta. A3, 39°16.5'N, 72°29.7'W, 136 m, 3 Nov. 1975—2

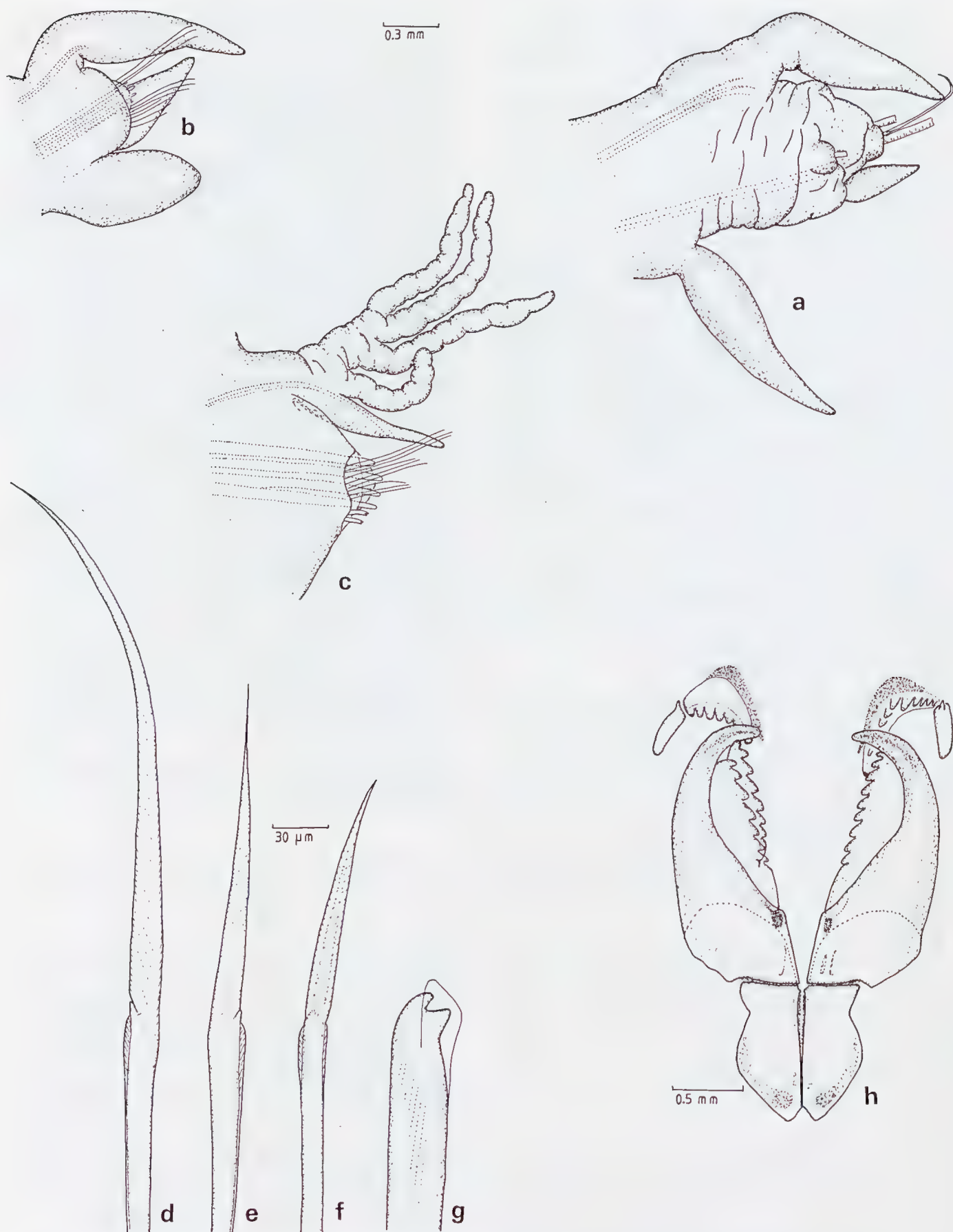


Fig. 8. *R. (Spinigerium) averincevi* (PML MU 68-29): a, parapodium 1, anterior view; b, parapodium 4, same view; c, parapodium 38, same view; d, pseudocompound lower limbate seta from setiger 6; e, pseudocompound cultriform limbate seta from setiger 19; f, pseudocompound spine-like seta from same; g, subacicular hook from setiger 38; h, maxillae.

(USNM 57040-1). South Carolina: *Pierce*, 32°30'N, 78°29'W, 218 m, 15 Feb. 1977—1 (USNM 060969) and 22 Aug. 1977—1 (USNM 060970). Florida: *Blake*, off Carysfort Reef, cast no. 4, 639 m, 31 Mar. 1869—1 (MCZ 779); *Blake* sta. 44, 25°33'N, 84°35'W, 986 m, 1878-79—2 (MCZ 754); *Columbus Iselin* sta. 2958, 25°40'N, 83°50'W, 120 m, Nov. 1977—1 (USNM 56142).

Diagnosis. Posterior antennae on median part of prostomium; branchiae from setiger 11–13, maximum of 5–6 filaments by setiger 30; falcigers present or absent on setiger 4; one subacicular hook from setiger 12–16, 2 from 17–18.

Description. Length to 38+ mm, number of setigers to 65+, width to 3 mm. Posterior antennae on median part of prostomium. Ceratophores of antennae with 2–4 proximal rings and long distal ring, styles subulate with threadlike ends, median style to setiger 2–4, posterior laterals to 3–5. No eyespots visible. Tentacular cirri

subulate. Each of parapodia 1–3 (Fig. 9a) with 3 short papilliform lobes and one longer postsetal lobe. From setiger 4 (Fig. 9b), low presetal and short rounded postsetal lobes, latter absent from about setiger 12. Dorsal cirri subulate. Single branchial filaments from setiger 11–13, bifid from 16–18, reaching maximum of 5–6 filaments by setiger 30.

Modified parapodia with long recurved hooks (Fig. 9c), setal sacs to about setiger 50. From setiger 4, upper bundle of pectinate (comb with 12–15 long teeth) and simple limbate setae projecting from dorsal pocket. Lower bundle of compound limbate setae; compound falcigers (Fig. 9d) present or absent. From setiger 5, only compound limbate setae in lower bundle, consisting of median (Fig. 9e) and cultriform (Fig. 9f) limbate setae, latter changing to weakly bilimbate spine-like (Fig. 9g) in following setigers. One bidentate subacicular hook from setiger 12–16, 2 from 17–18.

Mandibles calcified, shafts slender, cutting plates

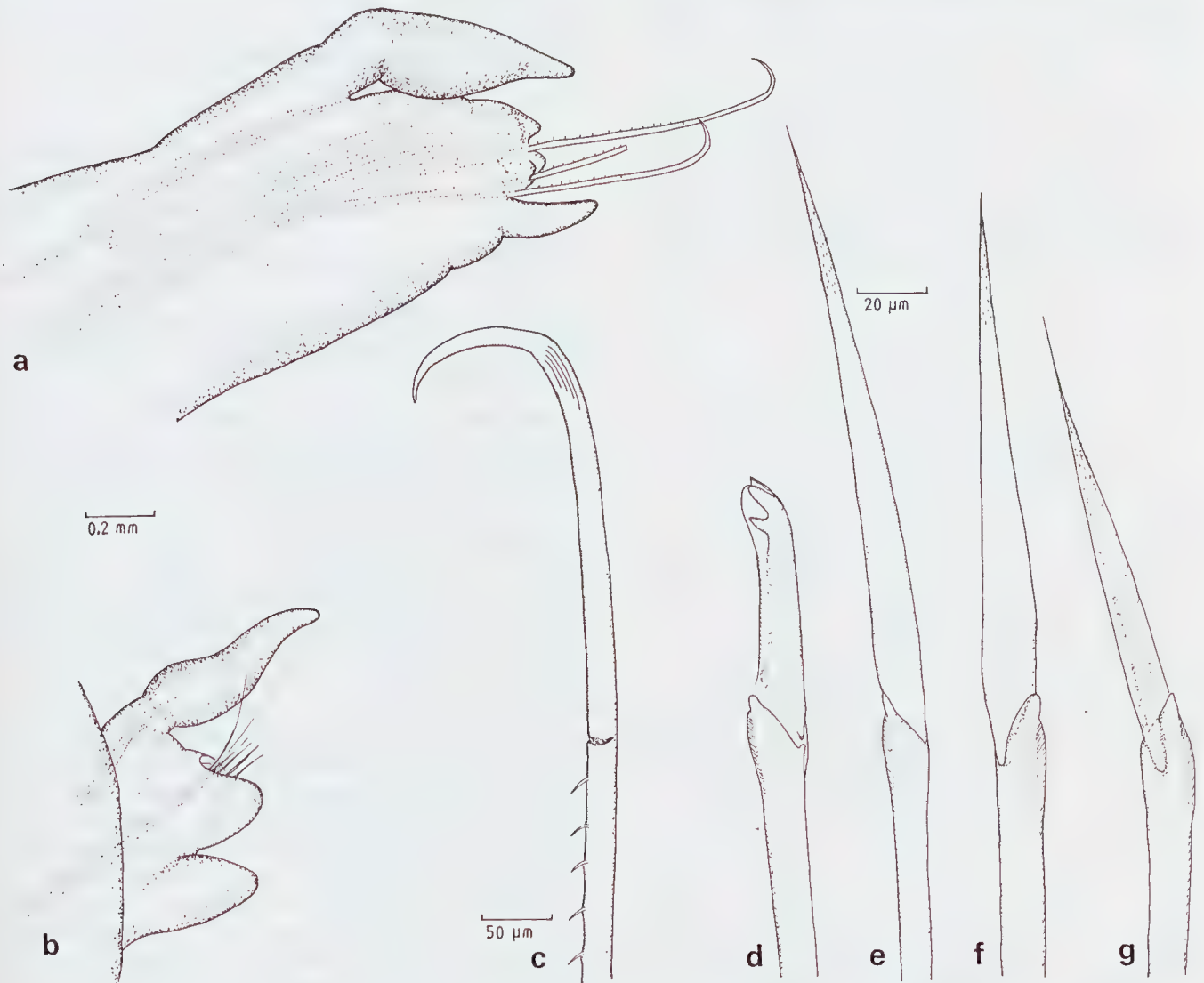


Fig. 9. *R. (Spinigerium) brevibrachiatum* (a,c,f,g: USNM 57040; b: MCZ 754; e,d: BMNH ZK 1921.5.1.1695): a, parapodium 2, posterior view; b, parapodium 4, same view; c, recurved seta from setiger 2; d, compound falciger from setiger 4; e, compound median limbate seta from same; f, compound cultriform limbate seta from setiger 16; g, compound spine-like limbate seta from same.

distally serrated. Maxillae very weakly sclerotized; maxillary formula: Mx I = 1 + 1; Mx II = 7–8 + 8; Mx III = 7–8 + 0; Mx IV = 5 + 8; Mx V = 1 + 1 (large plate). Inner layer of tubes parchment-like, covered on outside with foraminiferans and sand.

Remarks. The two syntypes of *Diopatra brevibrachiata* could not be located. Another specimen dredged by the *Porcupine*, 'probably between stations 46 and 47' (E of Strait of Gibraltar) according to McIntosh (1903), was examined. This specimen agreed in most respects with Ehlers' description and illustrations, and was considered as representative.

Ehlers (1875: figs 11–13) illustrated the ceratophores of the antennae as being totally ringed, thus representing 8 equal rings. This drawing is apparently incorrect since all species of *Rhamphobrachium* examined have a larger distal ring. In the specimens of *R.(S.) brevibrachiatum* examined, the distal ring made up more than half the length of the ceratophore. Ehlers stated that the filaments of the branchiae appeared to be arranged spirally. Although they are pectinate as stated by McIntosh (1903), they appear spiralled in some specimens due to constrictions of the main branchial stem.

Four specimens (MCZ 754, 779, 788) collected by the U.S. Coast Steamer *Blake* were included as syntypes of *R. agassizii* by Ehlers (1887). He remarked on their smaller size and considered them as juveniles. Ehlers considered long anterior modified parapodia as characteristic of *R. agassizii* and short ones of *R.*

brevibrachiatum since he was not aware of the degree to which they can be extended or retracted. He apparently did not check the setae of the unmodified segments which, in these specimens, do not have simple limbate setae like *R.(R.) agassizii*, but compound limbate setae like *R.(S.) brevibrachiatum*.

An interesting characteristic of *R.(S.) brevibrachiatum* is the fact that falcigers may be present or absent in setiger 4. The presence in one and absence in another, otherwise identical specimen from the same station has shown that the presence of falcigers is an unstable character in this species. Presumably they are present in all juveniles and are partially or completely replaced with spinigers in adults.

Rhamphobrachium (S.) brevibrachiatum is here newly reported from the western North Atlantic.

Biology. Several specimens contained sperm morulae and free spermatozoans. One specimen (USNM 57040) contained oocytes measuring 330 µm in diameter.

Distribution. Eastern North Atlantic: English Channel to Mediterranean; western North Atlantic: U.S.A. (off Virginia, South Carolina and Florida), ?NE South America; 120–1470 m.

Rhamphobrachium (Spinigerium) diversosetosum
Monro

Fig. 10a–d

Rhamphobrachium diversosetosum Monro, 1937: 295, text-fig. 17a–l (Maldives, 183–274 m).—Fauvel, 1953: 262, fig. 132c–h (same record).

Material examined. Maldives: John Murray sta. 164, 8°15'24"N, 73°01'30"E, 183 m—SYNTYPE (BMNH ZK 1937.9.2.380).

Diagnosis. Posterior antennae on median part of prostomium; branchiae from setiger 10, maximum of 8 filaments by setiger 30; falcigers on setiger 4; one subacicular hook from setiger 13, 2 from 14–15.

Description. Length to 30+ mm, number of setigers to 52+, width to 2.8 mm. Posterior antennae on median part of prostomium. Ceratophores of antennae with 3–4 proximal rings and long distal ring; styles slender, posterior styles to setiger 3–4. Small eyespots between bases of posterior and anterior lateral antennae. Tentacular cirri subulate.

Each of parapodia 1–3 with 3 short papilliform lobes and one longer postsetal lobe. On setiger 4, low presetal and short rounded postsetal lobes, latter absent from about setiger 12. Dorsal cirri subulate. Single branchial filaments from setiger 10, bifid from 14, maximum of 8 filaments by setiger 30.

Modified parapodia with long recurved hooks, setal sacs to about setiger 50. From setiger 4, upper bundle of simple limbate and pectinate setae (comb with 10–15 teeth); lower bundle of parapodia 4 with 2 compound limbate setae and about 15 compound falcigers (Fig. 10a). From setiger 5, only compound limbate setae in lower bundle, changing from cultriform (Fig. 10b) to bilimbate spine-like setae (Fig. 10c). One subacicular

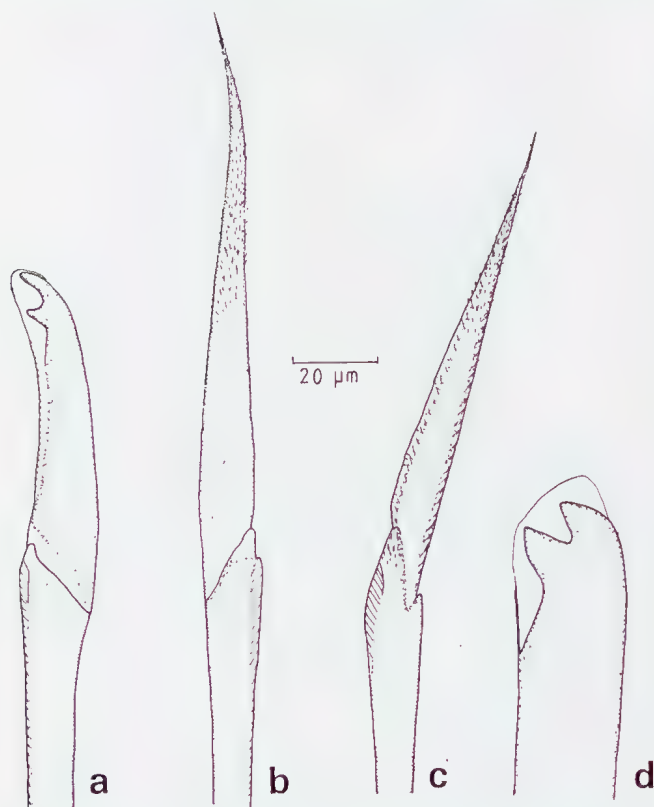


Fig. 10. *R. (Spinigerium) diversosetosum* (syntype BMNH ZK 1937.9.2.380): a, compound falciger from setiger 4; b, compound cultriform limbate seta from setiger 5; c, compound spine-like limbate seta from setiger 13; d, subacicular hook from setiger 14.

hook (Fig. 10d) from setiger 13, 2 from 14–15.

Mandibles calcified, shafts slender, cutting plates distally weakly serrated. Maxillae weakly sclerotized; maxillary formula: Mx I = 1 + 1; Mx II = 7 + 9; Mx III = 8 + 0; Mx IV = 7 + 7; Mx V = 1 + 1 (large plate). Tube unknown.

Remarks. *Rhamphobrachium* (*S.*) *diversosetosum* closely resembles *R.* (*S.*) *brevibrachiatum*. Both species have falcigers on setiger 4 and similar compound limbate setae. The two species can be distinguished in that: (1) falcigers in setiger 4 are more numerous; (2) subacicular hooks replace lower limbate setae earlier; and (3) branchiae start earlier and have more filaments in *R.* (*S.*) *diversosetosum* than in *R.* (*S.*) *brevibrachiatum* of a comparable size.

Distribution. Indian Ocean: Maldives; 183–274 m.

Rhamphobrachium (*Spinigerium*) *ehlersi* Monro

Fig. 11a–f

Rhamphobrachium ehlersi Monro, 1930: 126, fig. 46a–i (South Shetlands, Antarctica, 525 m); 1936: 148, fig. 27a–c (South Georgia).—Hartman, 1964: 117, pl. 36 figs 3–7 (previous records); Averincev, 1972: 182 (South Shetlands, South Orkneys).

Rhamphobrachium cf. *ehlersi*.—Hartman, 1967: 98 (South Shetlands, South Orkneys).

Rhamphobrachium golikovi Averincev, 1972: 183, pl. 36 fig. 1 (South Orkneys, 225 m).

Rhamphobrachium sp. Averincev, 1972: 184, pl. 36 fig. 2 (South Georgia).

Material examined. Antarctica: *Discovery* sta. 172, off Deception Island, South Shetlands, 62°59'S, 60°28'W, 525 m, 26 Feb. 1927—SYNTYPE (BMNH ZK 1930.10.8.1898/99); *Eltanin* sta. 410, South Shetlands, c. 61°18' to 61°20'S, 56°09' to 56°10'W, 220–240 m, 31 Dec. 1962—81 (USNM 58394); *Eltanin* sta. 1079, South Orkneys, c. 61°26' to 61°24'S, 41°55'W, 593–598 m, 13 Apr. 1964—1 (USNM 58395); *Eltanin* sta. 2198, Chathams, c. 43°48' to 43°48'S, 174°24' to 174°26'W, 881–909 m, 12 May 1968—1 (USNM).

Diagnosis. Posterior antennae on median part of prostomium; branchiae from setiger 10–12, maximum of 2 filaments by setiger 20; setiger 4 with short subulate postsetal lobes; one subacicular hook from setiger 15–16, 2 from 18–21.

Description. Length 26+ (to 45+) mm, setigers 35+ (to 72+), width 2.5 (to 3.5) mm. Flesh-coloured with traces of reddish brown pigment on prostomium and anterior parapodia. Posterior antennae on median part of prostomium. Ceratophores of antennae with 1–2 proximal rings and longer distal ring; styles short and subulate, posterior styles to setiger 2(1–2). Tentacular cirri subulate, slightly longer than posterior ceratophores.

Each of parapodia 1–3 with 3 short papilliform lobes and one slightly longer postsetal lobe. On setiger 4 (Fig. 11a), low presetal and short subulate postsetal lobes, latter reduced by setiger 8 and absent from 12. Dorsal cirri subulate. Single branchial filaments from setiger 10(10–12), maximum of 2 filaments from 19(about 20),

both filaments long, reaching further than dorsal midline, single again from about setiger 40.

Modified parapodia with long recurved hooks, setal sacs to about setiger 40. Pectinate (comb with 10–20 teeth) and simple long upper limbate setae from setiger 4. Lower bundle of weakly pseudocompound median and pseudocompound cultriform (Fig. 11b) limbate setae becoming gradually simple and shorter (Fig. 11c), and spine-like bilimbate (Fig. 11d) in following parapodia. One bidentate hooded subacicular hook (Fig. 11e) from setiger 15–16, 2 from 18–21.

Mandibles and maxillae greatly calcified, mandible strongly serrated at cutting edge (Fig. 11f), with slender shaft. Maxillary formula: Mx I = 1 + 1, Mx II = 7–9 + 7–9, Mx III = 5–9 + 0, Mx IV = 6–7 + 6–10, Mx V = 1 + 1 (large plate). Tubes with inner parchment-like layer and outer agglutinated sandgrains.

Remarks. Monro (1930: fig. 46a) illustrated setiger 4 and showed a presetal papilla. This papilla as such is not present in the syntype nor the other specimens examined. However, the presetal lobe is inflated, and the tip appears like an additional lobe when flattened on a slide (Fig. 11a). The inferior limbate setae (Fig. 11b) of setiger 4, described by Monro as compound, should be referred to as pseudocompound since there is no clear fracture.

Averincev (1972) described *R. golikovi* from the South Orkneys. He distinguished the new species from *R. ehlersi* in that the only specimen of the former lacked setae on setigers 1 and 2, and that the hooks of setiger 3 formed a loop at the base of the parapodium (Averincev, 1972: pl. 36 fig. 1). The absence of setae is probably due to parapodial regeneration or a case of abnormal development. Infrequently, looped hooks were also observed in the present study. They appear to occur when the hooks are withdrawn from the parapodium but the setal sac fails to retract sufficiently in the body cavity. *Rhamphobrachium golikovi*, which was collected in the same station as a specimen of *R.* (*S.*) *ehlersi* is considered a junior synonym of the latter.

Rhamphobrachium sp. was reported by Averincev (1972) from South Georgia. Although the 3 anterior parapodia contained hooks, only setigers 1 and 2 were enlarged and directed anteriorly (Averincev, 1972: pl. 36 fig. 2). Tentacular cirri were very small, branchiae occurred as single filaments from setigers 12–28. These features are in agreement with those of juveniles stage 4 of *R.* (*S.*) *ehlersi* (Paxton, 1986).

A poorly preserved specimen (*Eltanin* sta. 2198) is hesitantly referred to *R.* (*S.*) *ehlersi*. It agrees with all diagnostic characters of this species and also possesses the reddish pigment. However, it has slightly longer antennae with the proximal ceratophoral rings numbering 3–4 instead of 1–2. The specimen in question was collected near the Chatham Islands in the Pacific Ocean while all other specimens are from the Atlantic Ocean.

Biology. The *Eltanin* station 410 yielded 81 specimens ranging from 12 mm in length to adults. This material

made it possible to determine the sequence of ontogenetic changes the animals undergo from juvenile to adult morphology. The juvenile sequence has been divided into 4 stages (Paxton, 1986).

Many small specimens contained sperm morulae and free sperm. Oocytes (diameter 600 μm) were only found in one adult. The presence of sperm in juveniles suggests that *R. ehlersi* is a protandric hermaphrodite.

Distribution. South Atlantic Ocean: South Shetlands, South Orkneys, South Georgia, Antarctica; ?South Pacific Ocean: Chathams; 199–935 m.

Rhamphobrachium (Spinigerium) hutchingsae n. sp.

Fig. 12a–l

Material examined. Solomons: Malaita Island: NW coast, 1.2 km off Laulasi Village, S of Aoki, c. 400 m, bottom olive-gray sandy mud with coarse pebbles, 27 Aug. 1973, P.H. Colman, collector—HOLOTYPE (AM W.198968). Australia: Queensland: *Kimbla*, off Moreton Bay, 27°22'S, 153°37'E, 112–116 m, 29 Mar. 1969—PARATYPE (AM W.198969); *Kimbla* sta. 21, E of North Reef, 23°8.6'S, 152°16.6'E, 155 m, dead shell and fine sand and mud, 14 Dec. 1977—PARATYPE (USNM 98881); *Kimbla* sta. 22, Capricorn Channel, E of North West Island, 23°15.2'S, 152°24.1'E, 284 m, 14 Dec. 1977—PARATYPE (AM W. 17730). New South

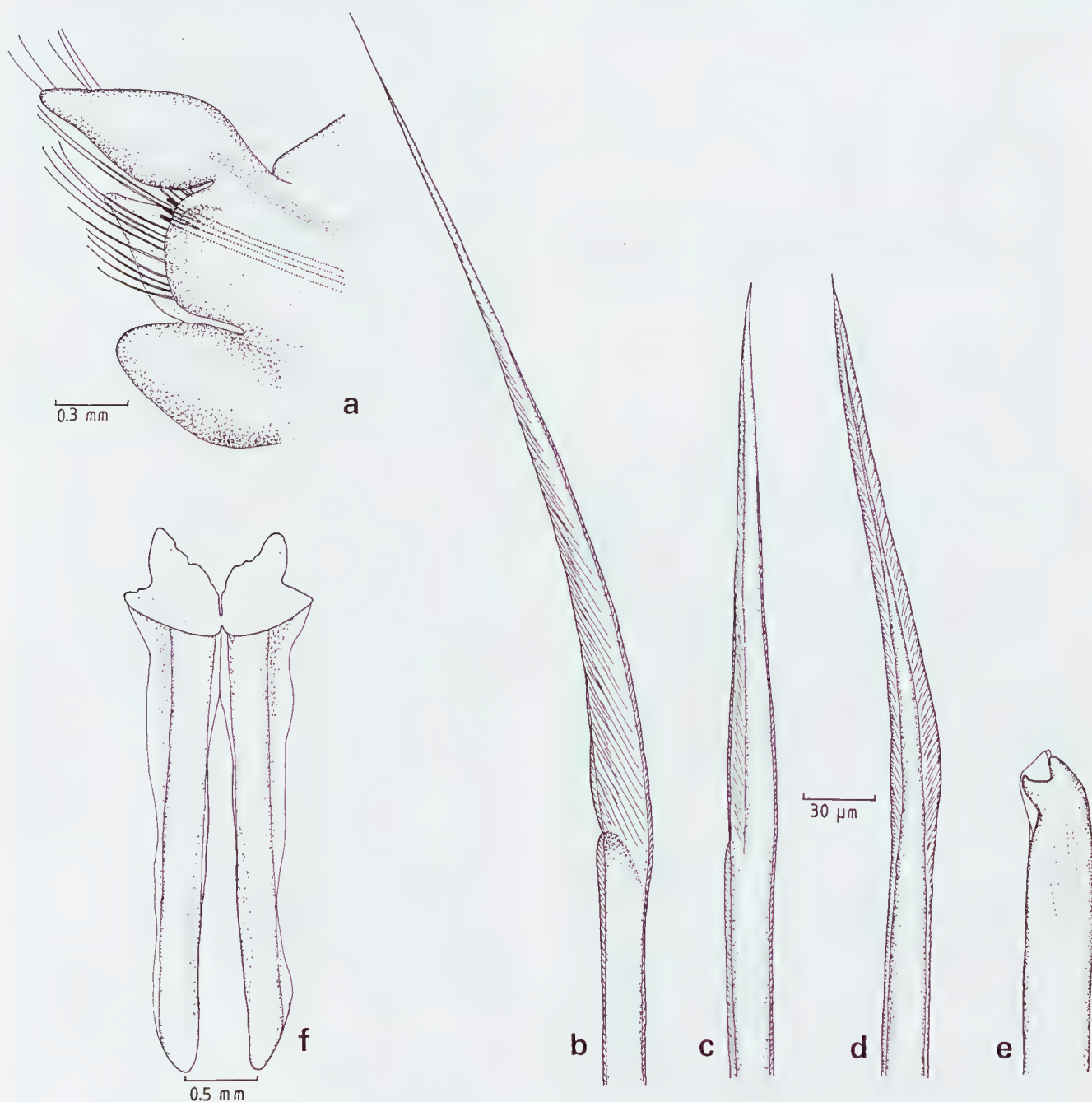


Fig. 11. *R. (Spinigerium) ehlersi* (USNM 58394): a, parapodium 4, anterior view; b, pseudocompound lower limbate seta from setiger 4; c, simple lower limbate seta from setiger 20; d, simple spine-like limbate seta from same; e, subacicular hook from setiger 27; f, mandibles.

Wales: Shelf Benthic Survey sta. 44, off Sydney, 33°58'54"S, 151°33'38"E, 187 m, 9 Aug. 1973—PARATYPE (AM W.6851).

Diagnosis. Posterior antennae on median part of prostomium; falcigers on setigers 4 and 5.

Description. Length 21 + (13 + -26 +) mm, number of setigers 44 + (29 + -70 +), width 2.0(2.0-2.8) mm. Holotype with brown pigmentation on prostomium (Fig. 12a) and anterior setigers, absent in paratypes. Posterior antennae on median part of prostomium. Ceratophores of antennae with 2(2-4) proximal rings and long distal ring. Styles subulate, posterior laterals to setiger 3(2-3), median to 2(1-2), anterior laterals to

1. Small eyespots between anterior and posterior lateral antennae. Tentacular cirri subulate, about as long as the ceratophores, inserted slightly subdistally on peristomium.

Each of parapodia 1-3 (Fig. 12b) with 3 short papilliform and one slightly longer subulate postsetal lobe. On setiger 4 (Fig. 12c), low presetal and short rounded postsetal lobes, latter absent from about setiger 20. Dorsal cirri subulate. Single branchial filaments from setiger 12(12-13), bifid from 17(19-23), reaching maximum of 4(2-5) filaments by about setiger 40.

Modified parapodia with long recurved hooks, setal sacs to about setiger 50. Acicula internal in modified

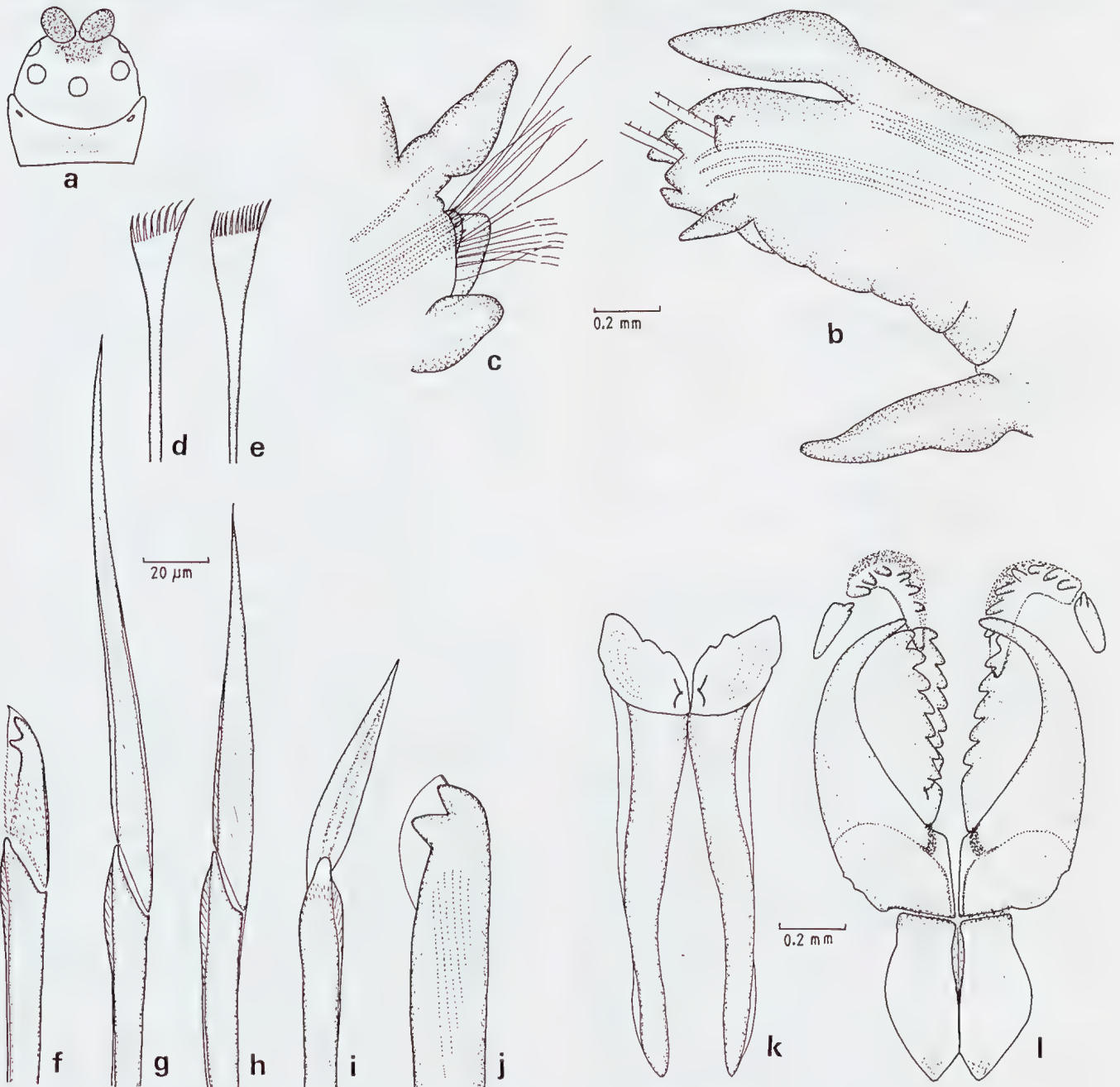


Fig. 12. *R. (Spinigerium) hutchingsae* (a, f-l: holotype AM W. 198968; b-e: paratype AM W. 6851): a, stylized diagram of prostomium and peristomium, showing pigmentation pattern, dorsal view; b, parapodium 2, posterior view; c, parapodium 4, anterior view; d, pectinate seta with 8 teeth from setiger 5; e, pectinate seta with 12 teeth from same; f, compound falciger from setiger 5; g, compound median limbate seta from setiger 6; h, compound cultriform limbate seta from same; i, compound spine-like limbate seta from setiger 13; j, subacicular hook from setiger 33; k, mandibles; l, maxillae.

parapodia, from setiger 4 with projecting rounded tip, numbering (3–4). From setiger 4, upper bundle of 1–3 pectinate setae (oblique comb with 8–12 long teeth) (Fig. 12d,e) and 6–8 simple long limbate setae projecting from dorsal pocket. Lower bundle of setiger 4 with 2 compound limbate and 10–12 compound falcigers (Fig. 12f); lower bundle of setiger 5 with limbate setae and 3–5 falcigers. From setiger 6, only compound limbate setae in lower bundle, consisting of compound median (Fig. 12g) and cultriform (Fig. 12h) limbate, becoming shorter and bilimbate spine-like (Fig. 12i) in following setigers. One subacicular hook (Fig. 12j) from setiger 12(13), 2 from 14(15–17).

Mandibles (Fig. 12k) with distally serrated cutting plates. Maxillae (Fig. 12l) weakly sclerotized; maxillary

formula: Mx I = 1 + 1; Mx II = 7 + 6; Mx III = 6 + 0; Mx IV = 6 + 7; Mx V = 1 + 1 (large plate). Tube unknown.

Etymology. The species is named in honour of Dr Pat Hutchings for her generous loans of specimens and other help during this study.

Remarks. *Rhaphobranchium* (S.) *hutchingsae* shares the possession of compound lower limbate setae and falcigers with *R.*(S.) *brevibrachiatum* and *R.*(S.) *diversosetosum*. However, it differs from both species in having falcigers on setigers 4 and 5, instead of only on setiger 4.

Biology. The holotype contains eggs (largest about 150 μ m diameter).

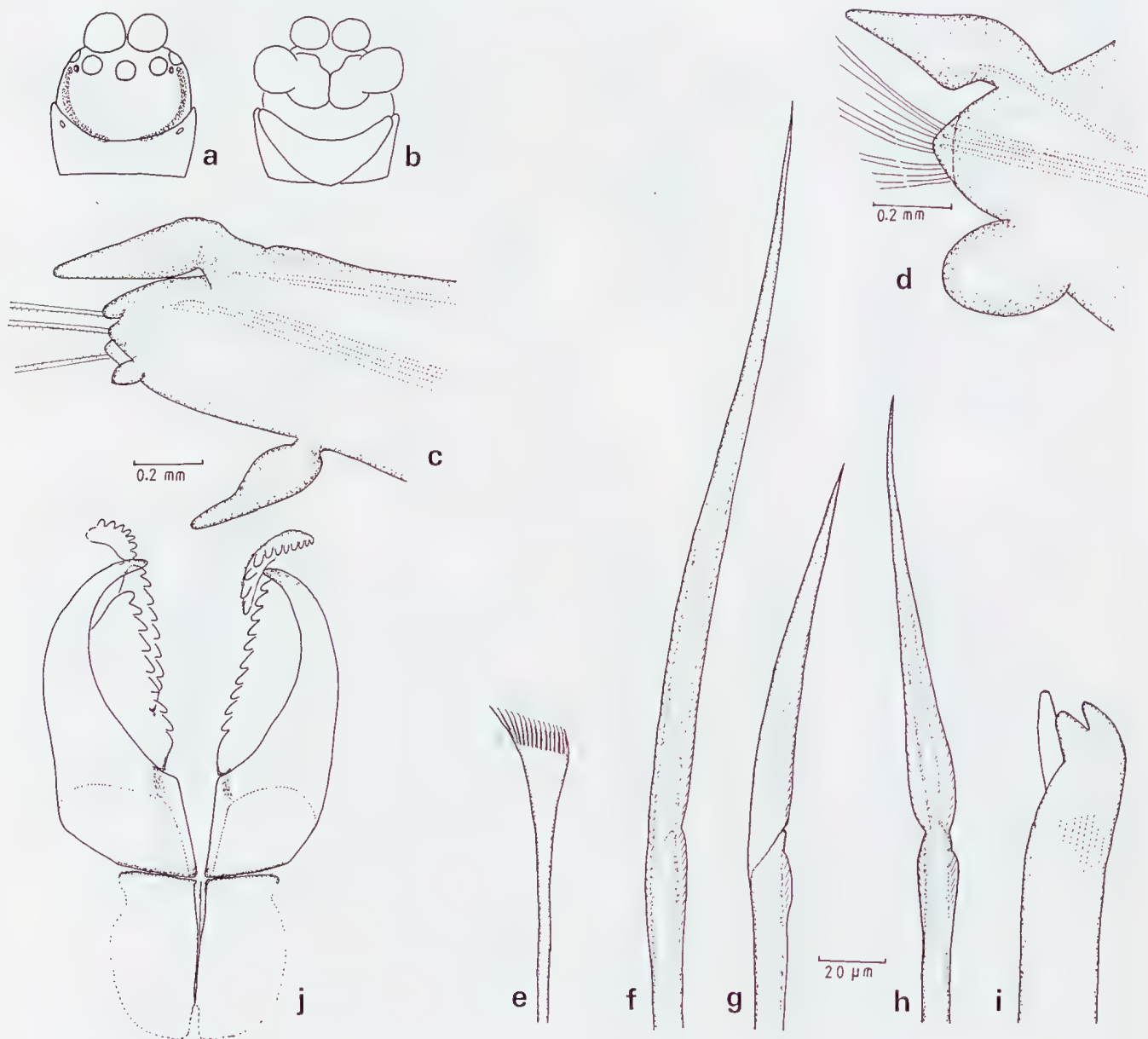


Fig. 13. *R. (Spinigerium) noeli* (c,e,i: paratype QM G10424; d,f–h: holotype QM G10436; j: paratype QM H569): a, stylized diagram of prostomium and peristomium, dorsal view; b, same, ventral view; c, parapodium 1, posterior view; d, parapodium 4, posterior view; e, pectinate seta from setiger 15; f, pseudocompound median limbate seta from setiger 4; g, compound cultriform limbate seta from same; h, compound spine-like limbate seta from setiger 5; i, subacicular hook from setiger 53; j, maxillae.

Distribution. South Pacific Ocean: Solomon Islands, Australia (Queensland and New South Wales).

Rhamphobranchium (Spinigerium) noeli n. sp.

Fig. 13a–j

Rhamphobranchium sp.—Stephenson *et al.*, 1974: 113 (Moreton Bay, Queensland, Australia).

Rhamphobranchium sp.—Day & Hutchings, 1979: 119 (same record).

Material examined. Australia: Queensland: Peel Island, Moreton Bay, 7.62 m, Sep. 1970, S. Cook, collector—HOLOTYPE (QM G10436); same locality and collector, 9.5 m, Jun. 1970—1 PARATYPE (QM G10424); same locality and collector, 6.4 m, Sep. 1970—2 PARATYPES (QM G10456 and G10483); Middle Banks, Moreton Bay, Dec. 1973, Dept. of Zoology, University of Queensland, collectors—1 PARATYPE (QM H571); same locality and collectors, Jun. 1974—1 PARATYPE (QM H569).

Diagnosis. Posterior antennae on anterior part of prostomium; branchiae from setiger 12–13, maximum of 4–5 filaments by setiger 30.

Description. Length 48(9 + –29 +) mm, number of setigers 155 (30 + –63 +), width 2.4(1.5–2.2) mm. Brown pigmentation on prostomium, antennae, palps and modified parapodia; pale in holotype, absent in some paratypes. Antennae positioned far anteriorly, leaving greater part of prostomium (Fig. 13a,b) exposed. Ceratophores of antennae with 2–3(2–4) proximal rings and long distal ring. Styles subulate; posterior styles to setiger 3(2–3), anterior laterals to 1. Eyes present between anterior and posterior lateral antennae; best developed in one paratype (QM G10424) where clear lenses are visible. Tentacular cirri subulate, slightly longer than ceratophores, inserted slightly subdistally on peristomium.

Each of parapodia 1–3 (Fig. 13c) with 3 short papilliform lobes and one rounded postsetal lobe of equal length. From setiger 4 (Fig. 13d), low presetal and short, rounded postsetal lobes, latter absent from about setiger 15. Dorsal and ventral cirri subulate, latter oval on setiger 4. Branchiae from setiger 12(12–13) as single filaments, bifid from setiger 22(18–19), maximum of 5(3–5) filaments by setiger 30(25–33), reduced to one by setiger 90, absent from last 50 setigers.

Modified parapodia with long, recurved hooks, setal sacs to about setiger 45. Acicula internal in modified parapodia, from setiger 4 with projecting rounded tip, numbering 3(3–4). From setiger 4, 1–3 distally oblique pectinate (comb with 10–15 long teeth) (Fig. 13e) and 5–7 long simple upper limbate setae. Lower bundle with 4–6 pseudocompound median (Fig. 13f) and 6–8 pseudocompound cultriform (Fig. 13g) limbate setae, becoming shorter and bilimbate spine-like (Fig. 13h) in following setigers. One bidentate hooded subacicular hook (Fig. 13i) from setiger 12(10–13), 2 from 16(15).

Pygidium with dorsal anus, and 2 dorsal (about as long as last 5 setigers) and 2 (half as long) ventral anal cirri. Calcified parts of mandibles dissolved; maxillae (QM H569) very weakly sclerotized (Fig. 13j). Maxillary

formula: Mx I = 1 + 1; Mx II = 8 + 10; Mx III = 7 + 0; Mx IV = 7 + 10; Mx V not observed. Tube with mucous inner layer and outer thin layer of pieces of shells and rubble.

Etymology. The new species is named in honour of Dr Noel N. Tait, supervisor and friend.

Remarks. *Rhamphobranchium (S.) noeli* approaches *R.(S.) verngreni*, another shallow water species, in its setal and branchial distribution. The two species can be easily distinguished by: (1) antennae positioned very far forward on the prostomium, and postsetal lobes of setiger 4 rounded (Fig. 13d) in the former; and (2) antennae positioned more medially, and postsetal lobes subulate (Fig. 16a) in the latter.

The new species is the only species of *Rhamphobranchium* encountered in the present study that has eyes with obvious lenses, and constructs tubes with a mucous rather than parchment-like lining.

Biology. In two specimens (QM G10424 and 10456) the body cavity was filled with eggs (largest 350 μ m in diameter) from about setiger 40.

Distribution. South Pacific Ocean: Australia (southern Queensland).

Rhamphobranchium (Spinigerium) pettiboneae n. sp.

Fig. 14a–k

Material examined. U.S.A.: Georgia: *Pierce* sta. 4G, c. 31°19'N, 79°28'W, 495 m, 23 Feb. 1977—HOLOTYPE (USNM 61025) and 2 PARATYPES (USNM 98879–80).

Diagnosis. Posterior antennae on anterior part of prostomium; branchiae from setiger 10–13, single filaments only.

Description. Length 27 (16 + –17 +) mm, number of setigers 61(38 + –40 +), width 1.3(1.2–1.9) mm. Colour markings consisting only of light brown pigment patches on palps, antennae, tentacular cirri and modified parapodia. Antennae positioned far anteriorly, leaving greater part of prostomium (Fig. 14a) exposed. Ceratophores of antennae with 1–3 irregular proximal rings and very long distal ring. Styles subulate; posterior laterals longest, to setiger 2–3, median to 1–2, anterior laterals to 1. No eyes visible. Tentacular cirri subulate, shorter than ceratophores, inserted subdistally on peristomium.

Each of parapodia 1–3 (Fig. 14b) with 3 short papilliform lobes and one longer subulate postsetal lobe. On setiger 4 (Fig. 14c), low presetal and short, rounded postsetal lobes, latter absent from about setiger 10–12. Dorsal cirri subulate, ventral cirri subulate on setigers 1–3, rounded on setiger 4. Branchiae from setiger 12(10–13), single filaments only; by setiger 20 about 3 times as long as dorsal cirrus, more posteriorly shorter, absent from about setiger 40.

Modified parapodia with long recurved hooks (Fig. 14d), setal sacs to about setiger 40. Acicula internal in modified parapodia, from setiger 4 with projecting rounded tip, numbering 2–3, becoming very thick after

setiger 10 (Fig. 14e). From setiger 4, 4–7 pectinate (comb with 15–20 teeth) (Fig. 14f) and 6–8 long simple upper limbate setae. Lower bundle with 4–5 weakly pseudocompound median and 5–6 pseudocompound cultriform (Fig. 14g) limbate setae, becoming spine-like (Fig. 14h) in following parapodia. One bidentate hooded

subacicular hook (Fig. 14i) from setiger 10(10–11), 2 from 11(13–14).

Pygidium with dorsal anus, and 2 long dorsal (about as long as last 7 setigers) and 2 very short ventral anal cirri (Fig. 14j). Mandibles with slender shaft, calcified cutting plates dissolved; maxillae (smaller paratype)

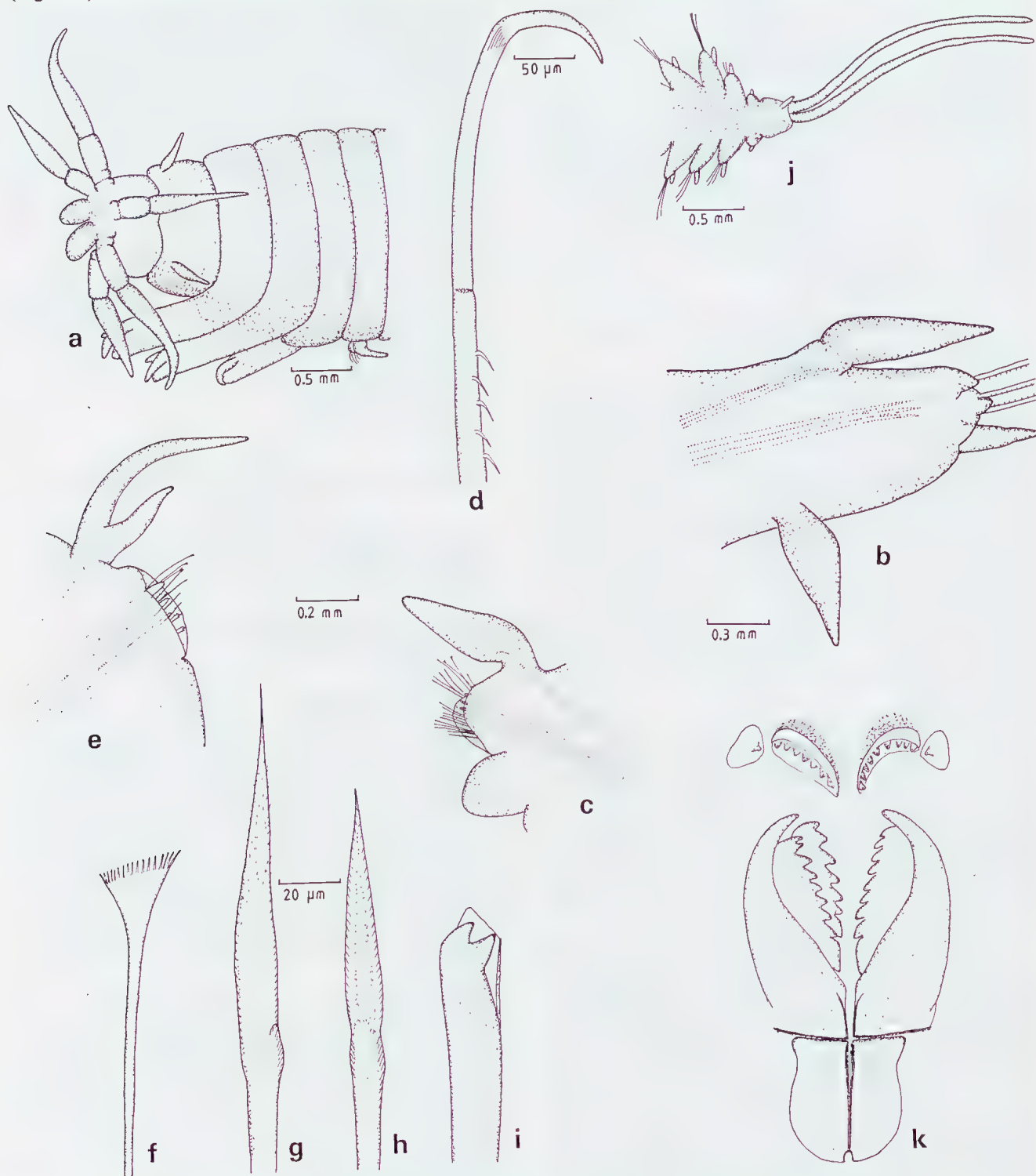


Fig. 14. *R. (Spinigerium) pettiboneae* (a,i,j: holotype USNM 61025; b,f,h,k: paratype USNM 98879; c-e,g: paratype USNM 98880): a, anterior end, dorsolateral view; b, parapodium 1, anterior view; c, parapodium 4, same view; d, recurved hook from setiger 1; e, parapodium 14, anterior view; f, pectinate seta from setiger 14; g, pseudocompound cultriform limbate seta from setiger 4; h, pseudocompound spine-like limbate seta from setiger 10; i, subacicular hook from setiger 12; j, posterior end, in ventral view; k, maxillae (Mx IV to Mx V not in natural position).

weakly sclerotized (Fig. 14k). Maxillary formula: Mx I = 1 + 1; Mx II = 8 + 8; Mx III = 6 + 0; Mx IV = 7 + 9; Mx V = 1 + 1 (large plate). Tube unknown.

Etymology. It gives me pleasure to name the new species in honour of Dr Marian H. Pettibone, whose help and advice I greatly appreciate.

Remarks. Although the types of *R.(S.) pettiboneae* are relatively small, they are adult specimens (see 'Biology' below). The new species shares the possession of pseudocompound lower limbate setae with *R.(S.) longisetosum*, *R.(S.) averincevi*, *R.(S.) verngreni*, *R.(S.) noeli*, *R.(S.) ehlersi* and *R.(S.) pyriforme*. *Rhamphobrachium (S.) pettiboneae* is distinguished from these species by being a very small species with such neotenic characteristics as ceratophores with few rings, single branchial filaments and early origin of subacicular hooks.

The occurrence of *R.(S.) pettiboneae* overlaps with the distribution of *R.(S.) brevibrachiatum*. The former differs mainly from the latter in that its lower limbate setae are pseudocompound instead of compound and its branchiae have only single filaments instead of 5–6.

Biology. Both paratypes contained free sperm and the holotype appeared to have spawned and retained some eggs, the largest of which had a diameter of 170 μ m. This evidence is taken as an indication that the specimens represent adults of a small species, rather than being juveniles.

Distribution. North Atlantic Ocean: U.S.A. (off Georgia); 495 m.

Rhamphobrachium (Spinigerium) pyriforme n. sp.

Fig. 15a–i

Material examined. Australia: New South Wales: Kapala sta. K78-27-04, 34°50'S, 151°15'E, c. 800 m, 12 Dec. 1978—HOLOTYPE (AM W.198978) and PARATYPE (AMS W.198979).

Diagnosis. Posterior antennae on median part of prostomium; branchiae from setiger 14, maximum of 2 filaments by setiger 20; setiger 4 with short subulate postsetal lobes; one subacicular hook from setiger 12–14, 2 from 15–16.

Description. Length 57 + (17 +) mm, number of setigers 73 + (35 +), width 4.0(2.2) mm. Reddish-brown pigment concentrated on palps, antennae, tentacular cirri, anterior parapodia, and as diffuse dorsal and ventral segmental bands. Posterior antennae on median part of prostomium. Ceratophores of antennae with closely spaced proximal rings and longer distal ring, lateral antennae with 3–4, median antenna with 2–3 proximal rings; styles of holotype cirriform, styles of paratype longer, with filiform ends; anterior lateral styles to setiger 1, posterior laterals to 3–4(6), median to 3(4). No eyes visible. Tentacular cirri subulate to pyriform, about as long as ceratophores.

Each of parapodia 1–3 (Fig. 15a) with 3 short papilliform lobes and one longer subulate postsetal lobe. On setiger 4 (Fig. 15b), low presetal and short subulate postsetal lobes, latter absent from about setiger 15. Anterior dorsal cirri of holotype pyriform, becoming gradually less inflated, subulate from setiger 10; in paratype subulate throughout. Ventral cirri pyriform to subulate on setigers 1–3, rounded on setiger 4. Branchiae from setiger 14 as single filaments; bifid from 21(16–17), single again from about setiger 50; posterior single filaments long, to middle of dorsum.

Modified parapodia with long recurved hooks, setal sacs to about setiger 40. Acicula internal in modified parapodia; from setiger 4, 4 projecting acicula: dorsalmost and presumably newest replacement aciculum with needle-like distal extension, broken off in older acicula, leaving rounded tips (Fig. 15c). In median and posterior region acicula large, reduced to 2 per parapodium (Fig. 15d). From setiger 4, 2–4 distally oblique pectinate (comb with 14–18 teeth) (Fig. 15e) and 8–10 long simple upper limbate setae. Lower bundle with 8–10 weakly pseudocompound median (Fig. 15f), and 8–10 weakly pseudocompound cultriform limbate setae (Fig. 15g), becoming shorter and almost simple bilimbate spine-like (Fig. 15h) in following parapodia. One bidentate hooded subacicular hook (Fig. 15i) from setiger 14(12), 2 from 16(15).

Calcified cutting plates of mandibles with tooth-like projections near point of fusion. Maxillae (paratype) weakly sclerotized; maxillary formula: Mx I = 1 + 1; Mx II = 7 + 7; Mx III = ? + 0; Mx IV = 6 + 8; Mx V = 1 + 1 (large plate). Tubes with tough parchment-like inner layer and outer thin layer of sand grains and foraminiferans.

Etymology. The name of the new species is derived from its characteristic pyriform cirri.

Remarks. *Rhamphobrachium (S.) pyriforme* is unique in that its tentacular cirri and anterior dorsal and ventral cirri are pyriform, a character that is more pronounced in the mature holotype than in the smaller paratype. The new species resembles *R.(S.) ehlersi* most closely in having some reddish-brown pigmentation and branchiae with only two but long filaments. The two species can be distinguished by: branchiae starting on setiger 14 in *R.(S.) pyriforme* and on setiger 10–12 in *R.(S.) ehlersi*; and antennae in the former being longer and having more rings than in the latter.

Biology. The holotype is ovigerous; the largest eggs measure 330 μ m in diameter.

Distribution. Pacific Ocean: eastern Australia; c. 800m.

Rhamphobrachium (Spinigerium) verngreni (Kinberg)

Fig. 16a–e

Onuphis Verngreni Kinberg, 1865: 560 (16 miles SE of Rio de Janeiro, Brazil, 106 m); 1910: 39, pl. 14 fig. 8 (same record).

Rhamphobrachium verngreni.—Augener, 1931: 295, fig. 4

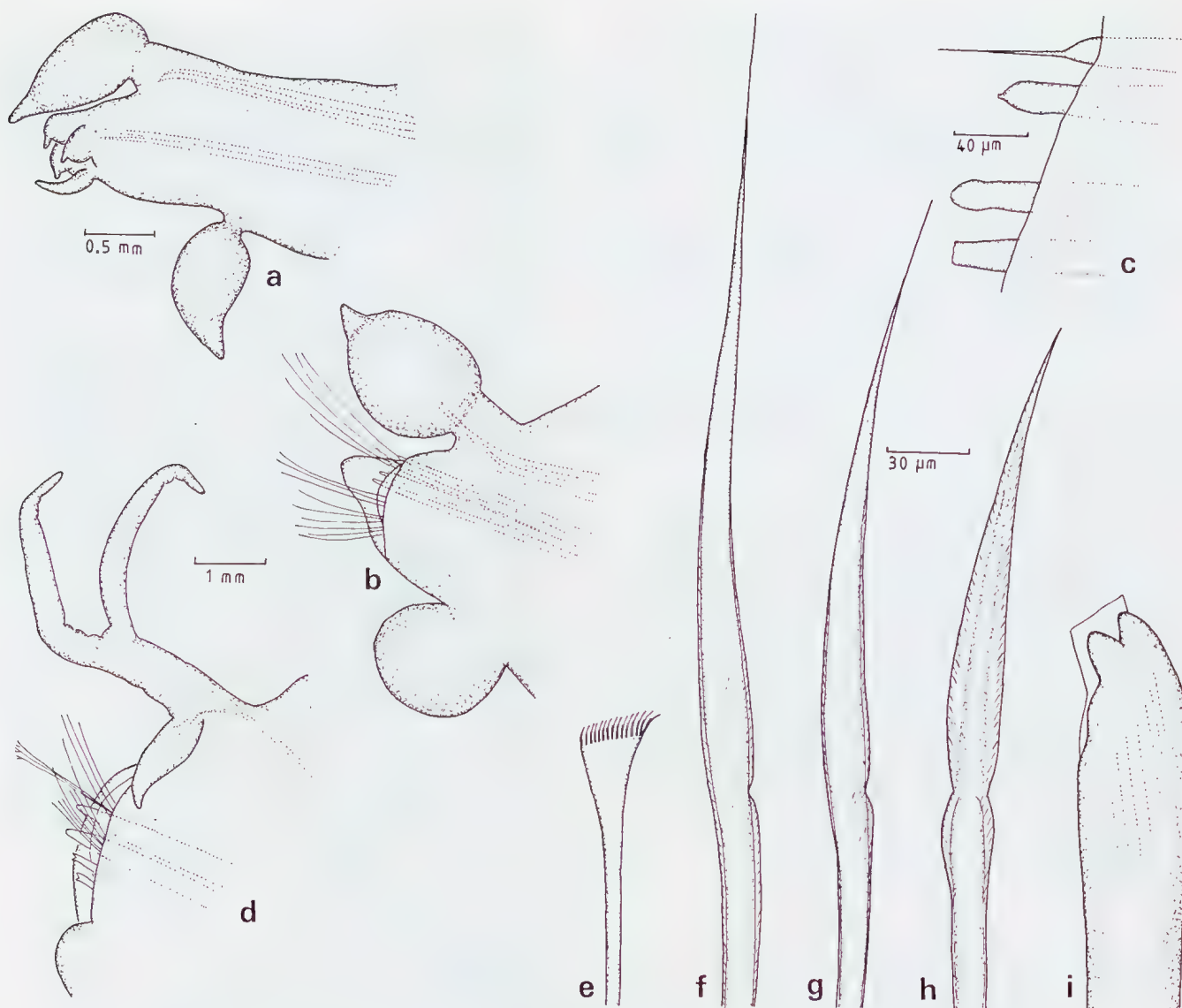


Fig. 15. *R. (Spinigerium) pyriforme* (holotype AM W.198978): a, parapodium 1, posterior view (pfl = papilliform lobes; psl = postsetal lobe); b, parapodium 4, anterior view; c, acicula from setiger 4; d, parapodium 33, anterior view; e, pectinate seta from setiger 33; f, pseudocompound median limbate seta from setiger 4; g, pseudocompound cultriform limbate seta from same; h, pseudocompound spine-like limbate seta from setiger 14; i, subacicular hook from setiger 33.

(examination of types); Orensanz, 1974: 109, pl. 11 figs 1–13 (Uruguay); Rullier & Amoureux, 1979: 176 (Brazil). [?] *Rhamphobranchium* sp. Orensanz, 1974: 112, pl. 12 figs 1–3 (Uruguay).

Material examined. Brazil: *Calypso* sta. 104, c. 23°08'S, 42°30'W, 103 m, 2 Dec. 1961–2 (MNHP AS278).

Diagnosis. Posterior antennae on median part of prostomium; branchiae from setiger 11–14, maximum of 4–7 filaments by setiger 35; setiger 4 with short subulate postsetal lobes; one subacicular hook from setiger 13–14, 2 from 17–18.

Description. Length to 34+ mm, setigers to 67+, width to 3 mm. No obvious pigmentation. Posterior antennae on median part of prostomium. Ceratophores of antennae with 2–3 proximal rings and longer distal ring; styles subulate, anterior lateral styles to setiger 1,

posterior styles to setiger 2–3. Tentacular cirri about as long as ceratophores.

Each of parapodia 1–3 with 3 short papilliform lobes and one slightly longer postsetal lobe. On setiger 4 (Fig. 16a), low presetal and short, subulate postsetal lobes, latter becoming reduced in following parapodia and absent from setiger 12–14. Dorsal cirri subulate. Single branchial filaments from setiger 11–14, bifid from 17–18, maximum of 4–7 filaments by setiger 35.

Modified parapodia with long recurved hooks, setal sacs to about setiger 55. From setiger 4, pectinate (comb with 10–15 teeth) and simple long upper limbate setae projecting from dorsal pocket. Lower bundle with weakly pseudocompound median and cultriform (Fig. 16b) limbate setae, becoming gradually shorter (Fig. 16c) and spine-like bilimbate (Fig. 16d) in following parapodia. One bidentate hooded subacicular hook from setiger 13–14, 2 from 17–18.

Calcified cutting plates of mandibles (Fig. 16e) with tooth-like projection at point of fusion. Maxillae hardly sclerotized, maxillary formula: Mx I = 1 + 1; Mx II = 7 + 6–8; Mx III = 5–6 + 0; Mx IV = 6 + 6–7; Mx V = 1 + 1 (large plate). Tubes with tough parchment-like inner layer and outer layer of mud, sand and shells.

Remarks. *Rhamphobrachium* sp. was reported by Orensanz (1974) from Uruguay in depths of 72–86 m. The presence of only 2 modified anterior pairs of

parapodia, compound limbate setae and bidentate falcigers in parapodia 3 (Orensanz, 1974: pl. 12) characterize the specimens as juveniles of *R. (Spinigerium)*. Since *R. (S.) verngreni* is the only known species of the genus to occur in the area, it is probable that the specimens belong to this species.

Distribution. South Atlantic Ocean: Brazil, Uruguay; in 72–115 m.

INCERTAE SEDIS

?*Rhamphobrachium (Spinigerium) bipes* Monro

Fig. 17a–d

Rhamphobrachium bipes Monro, 1937: 293, text-fig. 16a–h (Gulf of Aden, 91 m).

Paranorthia bipes.—Imajima & Hartman, 1964: 247 (new combination).

Material examined. Gulf of Aden: *John Murray* sta. 178, 12°00'36"N, 50°40'06"E, 91 m—HOLOTYPE (BMNH ZK 1937.9.2.378).

Diagnosis. Posterior antennae on median part of prostomium; branchiae from setiger 7, maximum of 5 filaments by setiger 40; falcigers on setiger 3; one subacicular hook from setiger 13, 2 from 14.

Description. Length 16+ mm, number of setigers 49+, width 1.5 mm. Ceratophores of antennae with 2–3 proximal rings and long distal ring; styles slender, posterior styles to setiger 2. Small eyespots between bases of posterior and anterior lateral antennae. Tentacular cirri subulate.

Each of parapodia 1–2 with 3 short papilliform lobes and one longer postsetal lobe. On setiger 3, low presetal and short rounded postsetal lobes, latter absent from about setiger 10. Dorsal cirri subulate. Single branchial filaments from setiger 7, bifid from 10, maximum of 5 filaments by setiger 40.

Two pairs of modified parapodia with long recurved hooks, setal sacs to about setiger 55. From setiger 3, upper bundle of simple limbate and pectinate setae (comb with 12 teeth). Lower bundle of parapodia 3 with compound falcigers (Fig. 17a); from setiger 4, compound cultriform limbate setae (Fig. 17b) in lower bundle changing gradually to bilimbate spine-like setae (Fig. 17c). One subacicular hook (Fig. 17d) from setiger 13, 2 from 14.

Mandibles and maxillae delicate, calcified, hardly sclerotized; maxillary formula: Mx I = 1 + 1; Mx II = 7 + 8; Mx III = 7 + 0; Mx IV = 7 + 8; Mx V = 1 + 1 (large plate). Tube unknown.

Remarks. The holotype of *R. (S.) bipes* displays the juvenile characteristics of only 2 modified pairs of parapodia and compound falcigers on setiger 3. It most closely resembles *R. (S.) diversosetosum* which possesses falcigers, compound limbate setae and well developed branchiae. It is possible that the holotype of *R. (S.) bipes* is a young *R. (S.) diversosetosum*. Although the material was collected on the same cruise of the *John Murray*, the stations are widely separated. Since *R. (S.) bipes*

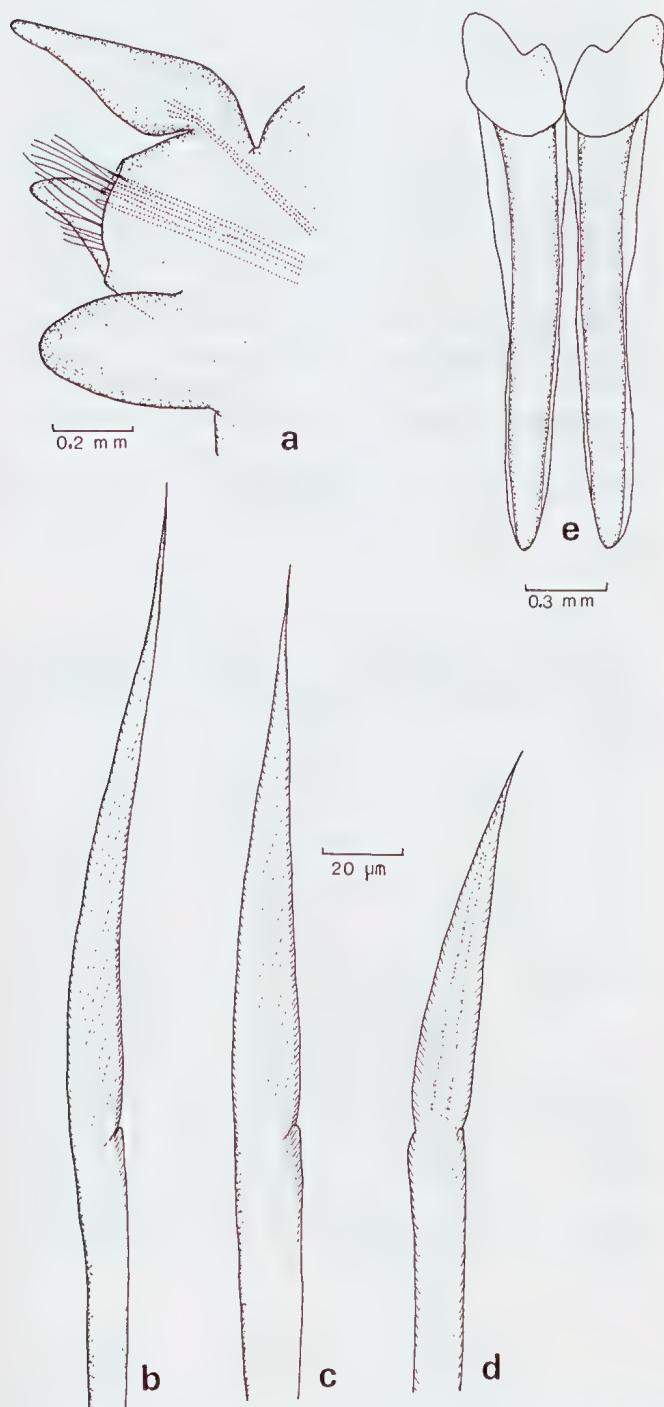


Fig. 16. *R. (Spinigerium) verngreni* (MNHN AS278): a, parapodium 4, anterior view; b, pseudocompound lower limbate seta from setiger 4; c, pseudocompound cultriform limbate seta from setiger 12; d, pseudocompound spine-like seta from same; e, mandibles.

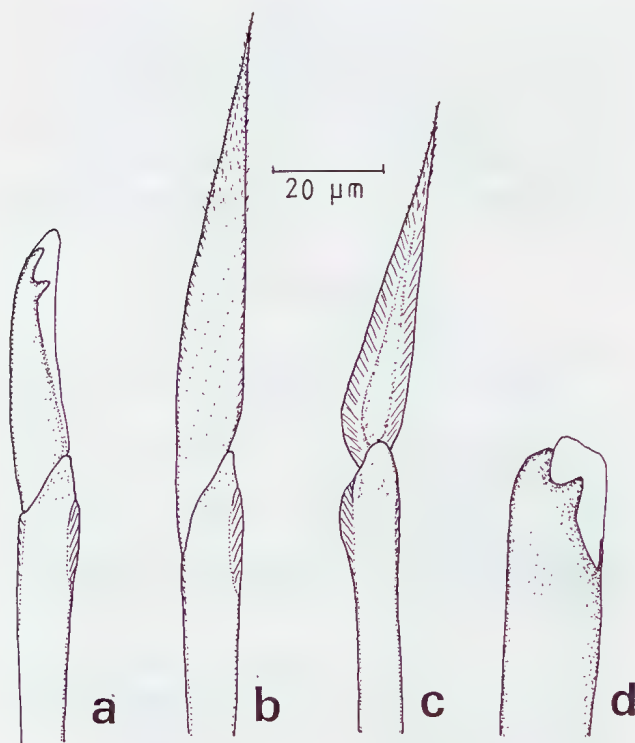


Fig. 17. *R. (Spinigerium) bipes* (holotype BMNH ZK 1937.9.2.378): a, compound falciger from setiger 3; b, compound cultriform limbate seta from setiger 5; c, compound spine-like limbate seta from setiger 9; d, subacicular hook from setiger 14.

cannot be positively identified with a known adult species, it is retained as a doubtful species.

Distribution. Indian Ocean: Gulf of Aden; 91 m.

Rhamphobranchium (Spinigerium) brevicornutum (Moore)

Fig. 18a,b

Paranorthia brevicornuta Moore, 1903: 448, pl. 25 figs 52–56 (Suruga Bay, Japan, 82–88 m).—Izuka, 1912: 108 (same record); Imajima & Hartman, 1964: 247 (same record). *Rhamphobranchium brevicornuta*.—Kucheruk, 1979b: 119 (new combination).

Material examined. Japan: Albatross sta. 3713, Suruga Bay, off Honshu Island, 82–88 m, 11 May 1900—HOLOTYPE (USNM 15712).

Diagnosis. Posterior antennae on median part of prostomium; branchiae from setiger 9, maximum of 2 filaments by setiger 23; falcigers on setiger 3; subacicular hooks from setiger 12–13.

Description. Length 13+ mm, number of setigers 44+, width 1.0 mm. Posterior antennae on median part of prostomium. Ceratophores of antennae with 1–2 proximal rings and long distal ring; styles subulate, to setiger 1. No eyes visible. Tentacular cirri subulate, shorter than ceratophores.

Each of parapodia 1–2 with 3 short papilliform lobes and one about equally long postsetal lobe. On setiger 3 (Fig. 18a), low presetal and short rounded postsetal

lobes, latter absent from about setiger 7–8. Dorsal cirri subulate. Single branchial filaments from setiger 9, bifid from 23.

Two pairs of modified parapodia with long spiny hooks (Fig. 18b). From setiger 3, upper bundle of 5 simple limbate setae. Lower bundle of parapodia 3 with 3 pseudocompound median limbate setae, 1 compound cultriform limbate seta and 6 compound falcigers; from setiger 4, only pseudocompound median, compound cultriform and spine-like limbate setae. Most anterior pectinate setae (comb with 15–20 long teeth) observed on setiger 7. Subacicular hooks from setiger 12–13.

Jaws not examined. Tube unknown.

Remarks. Although the distal parts of the long recurved hooks are broken off in the only type specimen, the long internal shafts bear the moveable spines, characteristic of *Rhamphobranchium*, clarifying its generic status (Paxton, 1986). The presence of only two modified pairs of parapodia marks the holotype of *R. (S.) brevicornutum* a juvenile. Since the type locality is widely separated from any other known species of *Rhamphobranchium*, *R. (S.) brevicornutum* remains an incompletely known species until more material becomes available.

Distribution. Eastern North Pacific: Japan; 82–88 m.

?*Rhamphobranchium (Spinigerium) cristobalensis* Fauchald

Rhamphobranchium cristobalensis Fauchald, 1968: 44, pl. 12 figs b–i (San Cristobel Bay, Baja California, 75 m).

Diagnosis. Antennae on anterior part of prostomium; branchiae from setiger 4, maximum of 2 filaments by setiger 18; falcigers on setiger 3; subacicular hooks from setiger 8.

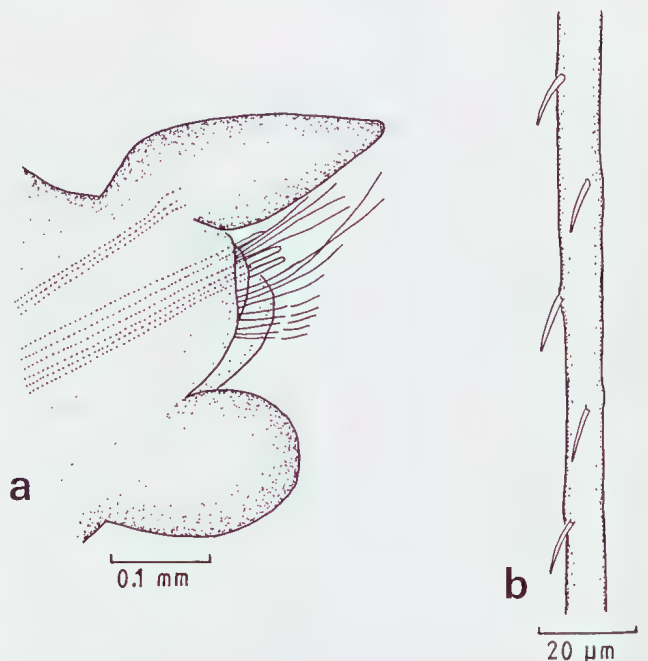


Fig. 18. *R. (Spinigerium) brevicornutum* (holotype USNM 15712): a, parapodium 3, anterior view; b, internal shaft of long spiny hook.

Description. Length 7 mm, number of setigers 63, width 1.2 mm with setae. Antennae on anterior part of prostomium. Ceratophores of antennae with 2–3 irregular rings; short styles, posterior styles to about setiger 3. Small anterior eyespots near frontal palps. Tentacular cirri longer than ceratophores, digitiform.

Each of parapodia 1–2 with 3 short papilliform lobes and one longer digitiform postsetal lobe. On setiger 3, low presetal and short rounded postsetal lobes. Dorsal cirri digitiform. Single branchial filaments from setiger 4, bifid from 18, single again from 33, absent from setiger 43.

Two pairs of modified parapodia with long recurved hooks, setal sacs to at least setiger 35. From setiger 3, upper bundle of simple limbate and lower bundle of compound limbate setae; compound falcigers in lower bundle of parapodia 3. Subacicular hooks from setiger 8. Pectinate setae in median and posterior region.

Maxillary formula: Mx I = 1 + 1; Mx II = 9 + 0; Mx III = 5 + 0; Mx IV = 0 + 5; Mx V = 0 + 0. Tube unknown.

Remarks. *Rhamphobrachium* (*S.*) *cristobalensis* is known only from two syntypes, both of which are juveniles. The specimens were collected within the geographic and depth distribution of *R. (S.) longisetosum* and may represent juveniles of that species. However, the con-specificity cannot be proven until a larger size range of juveniles becomes available.

Distribution. Pacific Ocean: Baja California; 75 m.

ACKNOWLEDGEMENTS. I sincerely thank my supervisor and friend, Noel N. Tait (MU), for his continued support and encouragement.

This study could not have been carried out without the generous help with loans and/or gifts of specimens by the following individuals: Susan J. Williams (AHF); Pat Hutchings (AM); David George and Alex Muir (BMNH); Herbert W. Levi, John M. Hunter and Ardis B. Johnston (MCZ); J. Renaud-Mornant (MNHP); Suzanne Boyd and Robin Wilson (NMV); P. K. Probert (NZOI); J. B. Jillett (PML); Patricia Mather (QM); Marian H. Pettibone and Kristian Fauchald (USNM); G. Hartwich (ZMB); Gesa Hartmann-Schröder (ZMH).

Special thanks are due to Marian H. Pettibone (USNM) for her generous help, encouragement, advice and review of the manuscript. I thank Walter Ivantsoff (MU) for translations, and Kristian Fauchald (USNM), Gesa Hartmann-Schröder (ZMH), Pat Hutchings (AM), and John R. Paxton (AM) for critical reviews of the manuscript.

The work was supported by a Commonwealth Postgraduate Research Award and Macquarie University Research Grants.

References

- Amoureux, L., 1972. Annélides polychètes recueillies sur les pentes du talus continental, au large de la Galice (Espagne). Campagnes 1967 et 1968 de la "Thalassa". Cahiers de Biologie Marine 13: 63–89.
- , 1974. Annélides polychètes recueillies sur les pentes du talus continental au nord-ouest de l'Espagne & du Portugal (campagne 1972 de la "Thalassa"). Cuadernos Ciencias Biológicas 3: 121–154.
- Augener, H., 1924. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. 18. Polychaeta II. Polychaeten von Neuseeland. I. Errantia. Videnskabelige Meddelelser fra Dansk naturhistorisk Føreling i Kjøbenhavn 75: 241–441.
- , 1927. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. 38. Polychaeten von Südost- und Süd-Australien. Videnskabelige Meddelelser fra Dansk naturhistorisk Føreling i Kjøbenhavn 83: 71–275.
- , 1931. Die bodensässigen Polychäten nebst einer Hirudinee der Meteor-Fahrt. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 44: 279–313.
- Averincev, V. G., 1972. Benthic polychaetes Errantia from the Antarctic and subantarctic collected by the Soviet Antarctic Expeditions. Explorations of the Fauna of the Seas 11(19), Biological Results of the Soviet Antarctic Expeditons 5: 88–293. (In Russian.)
- Bellan, G., 1964. Contribution à l'étude systématique, bionomique et écologique des annélides polychètes de la Méditerranée. Recueil des Travaux, Station Marine d'Endoume, Bulletin 33: 1–371.
- Berkeley E. & C. Berkeley, 1938. *Rhamphobrachium longisetosum*, sp. n., with some observations on the regeneration of the specialized anterior setae. Annals and Magazine of Natural History (London) (11) 1: 428–435.
- Day, J. H., 1960. The polychaet fauna of South Africa. Part 5. Errant species dredged off Cape coasts. Annals of the South African Museum 45: 261–373.
- , 1967. A monograph on the Polychaeta of southern Africa. Part I. Errantia. British Museum (Natural History) Publications 656: 1–458.
- , 1973. New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. National Oceanic and Atmospheric Administration Technical Report National Marine Fisheries Service Circular 375: i–xiii + 1–140.
- & P. A. Hutchings, 1979. An annotated check-list of Australian and New Zealand Polychaeta, Archiannelida and Myzostomida. Records of The Australian Museum 32(3): 80–161.
- Ehlers, E., 1875. Beiträge zur Kenntniss der Verticalverbreitung der Borstenwürmer im Meere. Zeitschrift für wissenschaftliche Zoologie 25: 1–102.
- , 1887. Reports on the results of dredging, under the direction of L.F. Pourtales, during the years 1868–1870, and of Alexander Agassiz, in the Gulf of Mexico (1877–78), and in the Caribbean Sea (1878–79), in the U.S. Coast Survey Steamer "Blake", Lieut.-Com. C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. 31. Report on the annelids. Memoirs of the Museum of Comparative Zoology at Harvard College 15: 1–335.
- , 1908. Die bodensässigen Anneliden aus den Sammlungen der deutschen Tiefsee-Expedition. Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899 16(1): 1–167.
- Estcourt, I.N., 1966. A new polychaete from Three Kings Islands. Transactions of the Royal Society of New Zealand. Zoology 7(15): 205–207.
- Fauchald, K., 1968. Onuphidae (Polychaeta) from western Mexico. Allan Hancock Monographs in Marine Biology 3: 1–82.
- Fauvel, P., 1914. Annélides polychètes non-pélagiques

- provenant des campagnes de l'*Hirondelle* et de la *Princesse-Alice* (1885-1910). Résultats des campagnes scientifiques accomplies sur son yacht par Albert Ier Prince Souverain de Monaco 46: 1-432.
- 1923. Polychètes errantes. Faune de France, Paris 5: 1-488.
- 1932. Annelida Polychaeta of the Indian Museum, Calcutta. Memoirs of the Indian Museum (Calcutta) 12(1): 1-252.
- 1953. The fauna of India including Pakistan, Ceylon, Burma and Malaya. Annelida Polychaeta. The Indian Press Ltd., Allahabad, pp. xii + 507.
- Gardiner, S.L., 1976. Errant polychaete annelids from North Carolina. Journal of the Elisha Mitchell Scientific Society 91(3): 77-220.
- Hartman, O., 1944. Polychaetous annelids. Part 5. Eunicea. Allan Hancock Pacific Expeditions 10: 1-238.
- 1959. Catalogue of the polychaetous annelids of the world. Allan Hancock Foundation Occasional Paper 23: 1-628.
- 1964. Polychaeta Errantia of Antarctica. Antarctic Research Series, American Geophysical Union 3: i-xi + 1-131.
- 1965. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. Allan Hancock Foundation Occasional Paper 28: 1-378.
- 1967. Polychaetous annelids collected by the USNS *Eltanin* and *Staten Island* cruises, chiefly from Antarctic seas. Allan Hancock Monographs in Marine Biology 2: 1-387.
- Hoagland, R.A., 1920. Polychaetous annelids collected by the United States Fisheries Steamer "Albatross" during the Philippine Expedition of 1907-1909. Bulletin of the United States National Museum 100 (vol. 1, part 9): 603-635.
- Imajima, M. & O. Hartman, 1964. The polychaetous annelids of Japan. Parts I & II. Allan Hancock Foundation Occasional Paper 26: 1-452.
- Intes, A. & P. Le Loeuff, 1975. Les annélides polychètes de Côte d'Ivoire. I.-Polychètes errantes-compte rendu systématique. Cahiers de la Office de la Recherche Scientifique et Technique des outre mer (Oceanographie) 13(4): 267-321.
- Izuka, A., 1912. The Errantiate Polychaeta of Japan. Tokyo University, College of Science Journal 30: 1-262.
- Kinberg, J.G.H., 1865. Annulata nova. Öfversigt af 'Kongliga Vetenskaps-Akademiens Förhandlingar (Stockholm) 21: 559-574.
- 1910. Annulater in 'Kongliga Svenska Fregatten *Eugenies* Resa omkring jorden under befäl af C. A. Virgin åren 1851-53' (ed. J.H. Theel). Vetenskapliga iakttagelser på Konung Oscar den Förstes Befallning utgifna delen, Zoologi 3: 33-78.
- Knox, G.A., 1960. The Polychaeta Errantia of the Chatham Islands 1954. expedition. New Zealand Department of Scientific and Industrial Research Bulletin 139: 77-141.
- & K. Hicks, 1973. The polychaetes of New Zealand. Part 5. Onuphidae. Journal of the Royal Society of New Zealand 3(2): 281-294.
- Kucheruk, N. V., 1979a. New species of the family Onuphidae (Polychaeta) from the Pacific. Zoologicheskyy Zhurnal, Akademia Nauk SSSR 58: 1227-1230. (In Russian.)
- 1979b. A new species of the genus *Rhamphobrachium* (Polychaeta, Onuphidae). Zoologicheskyy Zhurnal, Akademia Nauk SSSR 58: 119-121. (In Russian.)
- McIntosh, W.C., 1903. Notes from the Gatty Marine Laboratory, St. Andrews, no. 25. Annals and Magazine of Natural History (London) (7) 12: 128-166.
- 1910. A monograph of the British annelids. Polychaeta. Syllidae to Ariciidae. Ray Society (London) 2(2): 233-524.
- Monro, C.C.A., 1930. Polychaete worms. Discovery Reports 2: 1-222.
- 1936. Polychaete worms. II. Discovery Reports 12: 59-198.
- 1937. Polychaeta. The John Murray Expedition 1933-34 Scientific Reports 4(8): 243-321.
- Moore, J.P., 1903. Polychaeta from the coastal slope of Japan and from Kamchatka and Bering Sea. Proceedings of the Academy of Natural Sciences of Philadelphia 55(2): 401-490.
- Orensanz, J.M., 1974. Los anelidos poliquetos de la provincia biogeografica Argentina. V. Onuphidae. Physis (Buenos Aires) A33(86): 75-122.
- Paxton, H., 1986. Generic revision and relationships of the family Onuphidae (Annelida: Polychaeta). Records of the Australian Museum 38(1): 1-74.
- Pettibone, M.H., 1967. Type-specimens of polychaetes described by Edith and Cyril Berkeley (1923-1964). Proceedings of the United States National Museum 119(3553): 1-23.
- Rullier, F. & L. Amoureux, 1979. Campagne de la *Calypso* au large des côtes Atlantiques de l'Amérique du Sud (1961-1962). I. 33 Annélides Polychètes. Annales Institut Océanographie 55: 145-206.
- Smith, B.J. & R.L. Jenz, 1968. Unusual mode of reproduction in a new species of polychaete. Nature 218: 777.
- Stephenson, W., W.T. Williams & S.D. Cook, 1974. The benthic fauna of soft bottoms, southern Moreton Bay. Memoirs of the Queensland Museum 17(1): 73-123.
- Stull, J., 1979. Some benthic polychaetes from New Zealand. New Zealand Oceanographic Institute Records 4(5): 24-43.
- Treadwell, A.L., 1939. Polychaetous annelids of Porto Rico and vicinity. Scientific Survey of Porto Rico and the Virgin Islands. New York Academy of Sciences 16(2): 151-319.

Accepted 2 December 1985

A Revision of the Genus *Euthelepus* (Terebellidae: Thelepininae)

PAT HUTCHINGS AND CHRIS GLASBY

Australian Museum,
P.O. Box A285, Sydney South, NSW 2000, Australia

ABSTRACT. The genus *Euthelepus* is redefined, and of the 7 species currently assigned to it only 2 species belong to the genus, plus a newly described species *E. serratus* n.sp. The remaining species belong either to *Thelepus* or *Streblosoma*. A full description of each species is given where necessary, based upon a re-examination of type material. A key to the species of *Euthelepus* is given. Comments are made upon the validity of some of the characters which have been used traditionally in terebellid taxonomy.

HUTCHINGS, P.A. & C.J. GLASBY, 1986. A revision of the genus *Euthelepus* (Terebellidae: Thelepininae). Records of the Australian Museum 38(2): 105–117.

The genus *Euthelepus* was erected by McIntosh (1885) for *E. setubalensis*, and since then 7 other species have been assigned to the genus, plus the new species *E. serratus* described in this paper. However, on examining the literature it became apparent that *Euthelepus* was a mixture of species belonging to several genera. We therefore decided to examine type material of all the species which had been assigned to the genus, redescribe the species where necessary and assign it to correct genus.

Of the eight species which have been assigned to this genus, two species—*E. setubalensis* McIntosh, 1885, the type species, and *E. kinsemboensis* Augener, 1918—belong to the genus *Euthelepus*, plus a new species described in this paper. The remaining 6 species belong to either *Thelepus* (*E. malayensis* Caullery, 1944, *E. tenuis* (Verrill, 1900), *E. abbranchiatus* Hartman & Fauchald, 1971 and *E. pascua* Fauchald, 1977a) or *Streblosoma* (*E. chilensis* McIntosh, 1885 and *E. atlanticus* Hartman & Fauchald, 1971). This has also necessitated the redefining of the genus *Euthelepus* and in the Discussion we comment on the usefulness of some of the generic characters which have been used in the subfamily Thelepininae.

The following abbreviations have been used in the text:

AHF Allan Hancock Foundation, Los Angeles

- AM The Australian Museum, Sydney
- BMNH British Museum of Natural History, London
- HZM Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Hamburg
- USNM National Museum of Natural History, Washington, D.C.
- YPM Peabody Museum of Natural History, Yale University, New Haven
- ZMA Zoologisch Museum, Universiteit van Amsterdam, Amsterdam.

TAXONOMIC ACCOUNT

Genus *Euthelepus* McIntosh

Euthelepus McIntosh, 1885:465.

Type species. *E. setubalensis* McIntosh

Prostomium compact, with numerous grooved buccal tentacles. Three pairs of long, thick filaments, relatively sparse in number on segments 2, 3 and 4. Notosetae present from segment 3 and continuing for a variable number of segments. Notosetae either all smooth-tipped or a mixture of smooth-tipped and serrated setae. Neurosetae present from segment 5, continuing to pygidium; uncini with dorsal attachment button. Lateral lobes present on segments 2–3 and sometimes 4.

Key to species of *Euthelepus*

1. All notosetae smooth-tipped. ... *E. setubalensis*
 — Notosetae of 2 kinds, smooth- and serrate-tipped. 2
2. Small, digitiform post-setal lobe present on some anterior notopodia. . *E. kinsemboensis*
 — Post-setal lobe absent on anterior notopodia. *E. serratus* n.sp.

Euthelepus kinsemboensis Augener

Figs 1a-d; 4a

Euthelepus kinsemboensis Augener, 1918: 548, pl. 6 fig. 161, pl. 7 fig. 250, text-fig. 93; Fauvel, 1930: 553-4, fig. IX a-f; Day, 1967: 726, fig. 36.5 e-i.

Material examined. HOLOTYPE (HZM V896): Kinsembo, Angola, coll. A. Hupfer; consists of two fragments, an anterior one of 2.5 mm length, 12 setigers, 0.7 mm width in good condition and a posterior fragment about 2.0 mm long, 7 setigers, 0.4 mm width extremely flattened, in poor condition.

Description. Body slender, brittle. Prostomium obscured. Buccal tentacles thick, deeply grooved, with a crenate margin, extending beyond setiger 12. Eyespots not visible. Peristomium ventrally with a shelf-like lower lip; a deep cleft separating the peristomium from segment 2 ventrally (Fig. 1a). Lateral lobes small, 2 pairs, present on segments 2 and 3, anterior pair slightly larger and slightly ventrally displaced; a third pair of very small lateral lobes present on segment 4. Branchiae long, with slightly tapered filaments on segments 2-4 arranged as follows: segment 2, 6 in a continuous line;

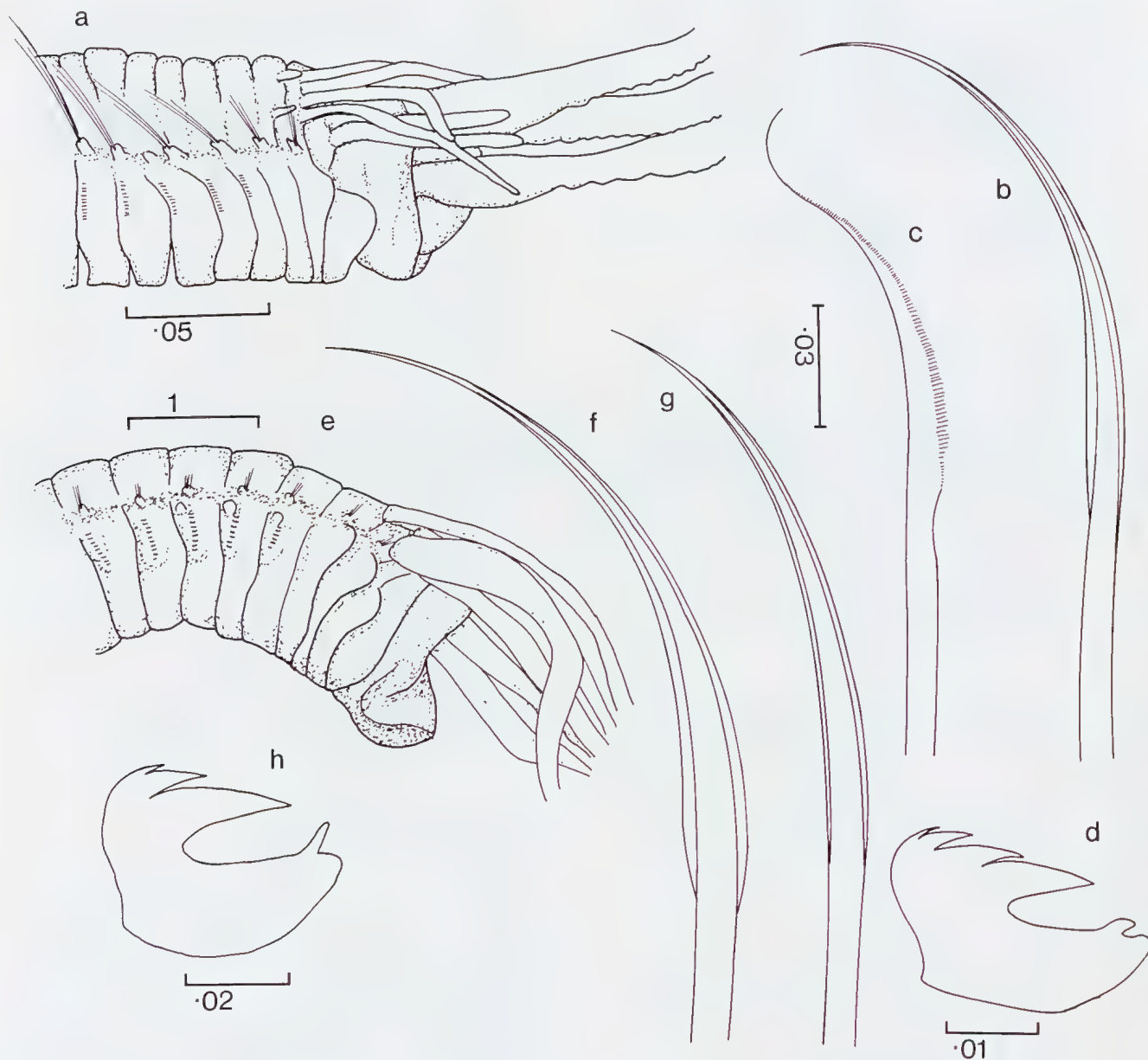


Fig. 1. *Euthelepus kinsemboensis*, holotype: a, head end, dorsolateral view; b, c, two types of notosetae from setiger 12; d, uncinus from setiger 12. *Euthelepus setubalensis*, holotype: e, head end, lateral view; f, g, two notosetae from setiger 10; h, anterior uncinus. All measurements in mm.

segment 3, 4 in a continuous line; segment 4, 2 filaments, with a very small medial gap.

Notosetae from segment 3, extending for at least 19 setigers; two types including smooth, broad winged capillaries and finely serrated capillaries of similar length (Fig. 1b,c). Notopodia of at least first 12 setigers with small, digitiform post-setal lobes. Avicular uncini from segment 5, arranged in single, short rows. Uncini with a hooked dorsal button and pointed prow (Figs 1d; 4a); dental formula of anterior uncini varying within a row as follows: MF:2:3:6–10 with the most distal row possibly comprising two rows. Uncinial tori low, rectangular. Nephridial papillae absent. Ventral pads distinct on segments 5–13.

Comments. *Euthelepus kinsemboensis* most closely resembles the new species, *E. serratus* n.sp., in having serrated as well as smooth notosetae. The serrated notosetae in this species, however, are the same length as the smooth type, not shorter as in *E. serratus* n.sp.

Day (1967) suggests that *E. kinsemboensis* should possibly be transferred to the genus *Amphitrite* which also has serrated notosetae and lateral lobes, even though in *Amphitrite* the first notosetae start on segment 4 (seg. 3 in *Euthelepus*). We feel however, that the segment on which the notosetae begin is an important generic character, at least in adult animals. In addition, *E. kinsemboensis* would seem to share more characters in common with *Euthelepus* (presence of lateral lobes, notosetae from segment 3, uncini from segment 5, 3 pairs of branchiae, form of uncini, form of serrated notosetae) than with *Amphitrite*. The serrated notosetae in *E. kinsemboensis* and probably in Thelepininae in general appear to be quite different from those in the Amphitritinae.

Habitat. Littoral and sub-littoral, coral reefs at Ile des Pins.

Distribution. Angola; Ile des Pins, New Caledonia.

Euthelepus serratus n.sp.

Figs 2a–e; 4b; Pl. 1a–f

Material examined. HOLOTYPE: Wreck Bay, New South Wales, 150°37'E 35°20'S (AM W199007) complete, 82 setigers, 54 mm long, 2.2 mm wide (maximum). PARATYPES: Port Gregory, Western Australia, 114°15'E 28°12'S, 1(AM W5443), 1(USNM 97887); Two Islands, Great Barrier Reef, Queensland 15°09'S 145°27'E 1(BMNH ZB 1985. 95). Paratypes incomplete, ranging in width from 1.6–2.2 mm.

Description. Body long, uniformly slender throughout. Prostomium large, horse-shoe shaped, slightly inflated with smooth surface, posteriorly forming a tentacular ring, slightly deflated posteriorly. Tentacles with a deep medial groove and crenate margins arising from anterior edge of tentacular ring. Posterior edge of tentacular ring with numerous small, red eyespots in a broad band, widest laterally. Peristomium equal in length to segment 2, with a thickened anterior margin on dorsal surface, ventrally forming a large, plaque-like lower lip (Fig. 2a).

Branchiae arising from anterior margin of segments 2–4, short, tapered with many irregular transverse wrinkles. Numbers of filaments on segments 2–4 respectively as follows: 13, 8, 4; filaments extending across dorsum in 1 row on segments 2, 3, without medial gap; on segment 4 a small medial gap present. Two pairs of small lateral lobes on segments 2–4, extending slightly ventrally, each with a crenate margin.

Notosetae from segment 3, extending for 44 setigers, of two types including long, smooth, narrow-winged capillaries and shorter, finely serrated capillaries (Fig. 2b,c; Pl. 1a–e). Notopodial lobes elongate, rectangular throughout with glandular pocket at base. Avicular uncini from segment 5, arranged in single, straight to slightly curved rows to pygidial segment; uncinial rows in posterior part of abdomen about $\frac{1}{3}$ length of thoracic ones. Uncini with prominent, hooked dorsal button (Figs 2d,e; 4b), dental formulae variable, with a row as follows: MF:2:1–2 (anterior rows), MF:2:2–4:4–6 (posterior rows) (Pl. 1f). Uncinigerous tori on glandular pads, slightly raised from body wall throughout, decreasing in size posteriorly.

Nephridial papillae absent. Ventral pads distinctly glandular on segments 2–10, thereafter ventrum increasingly dissected, glandular to setiger 24, followed by a narrow medial groove to near pygidium.

Variation. The paratype material generally resembles the holotype closely. The dorsal surface of the prostomium appears papillate in some specimens. The number of eyespots in the Queensland specimen is considerably fewer and they are absent on the medial portion of the tentacular ring. Branchial filaments short, tapered in all specimens, varying in number as follows: segment 2, 11–14; segment 3, 8–9; segment 4, 2–4. Lateral lobes often smooth, without crenate margin.

The number of pairs of notosetae ranges from 32–42. Uncini taken from setiger 5 and a posterior setiger show the following variation between animals: MF:2–3:1–2 (setiger 5), MF:2–4:3–6:4–10 (posterior rows). The abdominal uncinial tori in the specimens from Port Gregory (AM W5443) are slightly more elongate than in the holotype, reaching $\frac{1}{3}$ the body width in some far posterior setigers.

Comments. *Euthelepus serratus* shows typical characters of the genus, i.e. branchiae on segments 2–4, lateral lobes present, notosetae from the second branchial segment (segment 3), and uncini present from the first post-branchial segment (segment 5) (after Fauchald, 1977b). Like *E. kinsemboensis*, however, it differs from the type species in having serrated as well as smooth notosetae. Although the presence of such setae is often considered of generic importance in the Amphitritinae, it is not thought to be the case in the Thelepininae (see Discussion). The serrated notosetae of *Euthelepus serratus* are quite different from anything found in the Amphitritinae and are thought to represent an extreme example of a modified smooth seta in which the chiton layers comprising the blade have separated (Pl. 1a, b). For this reason the species is put into the

genus *Euthelepus*.

The holotype of *E. kinsemboensis* was also examined and compared with the new species. *Euthelepus kinsemboensis* differs from *E. serratus* in having post-setal notopodial lobes in some anterior setigers, and in the form of the notosetae. In *E. kinsemboensis*, the serrated notosetae are the same length as the smooth notosetae whereas in *E. serratus* n.sp. the serrated type is considerably shorter. In addition, the smooth notosetae in *E. kinsemboensis* have greater development of the wing than in the new species. The form of the uncini in both species is very similar.

The apparently discontinuous distribution of the species probably reflects the lack of subtidal collecting which has occurred off the Australian coast.

Habitat. Rocky substrates, often associated with detritus, 1–20 m.

Distribution. Australia (Port Gregory, Western Australia; Wreck Bay, New South Wales; Two Isles, Queensland).

Etymology. The specific name *serratus* refers to the serrated notosetae, and is a Latin adjective.

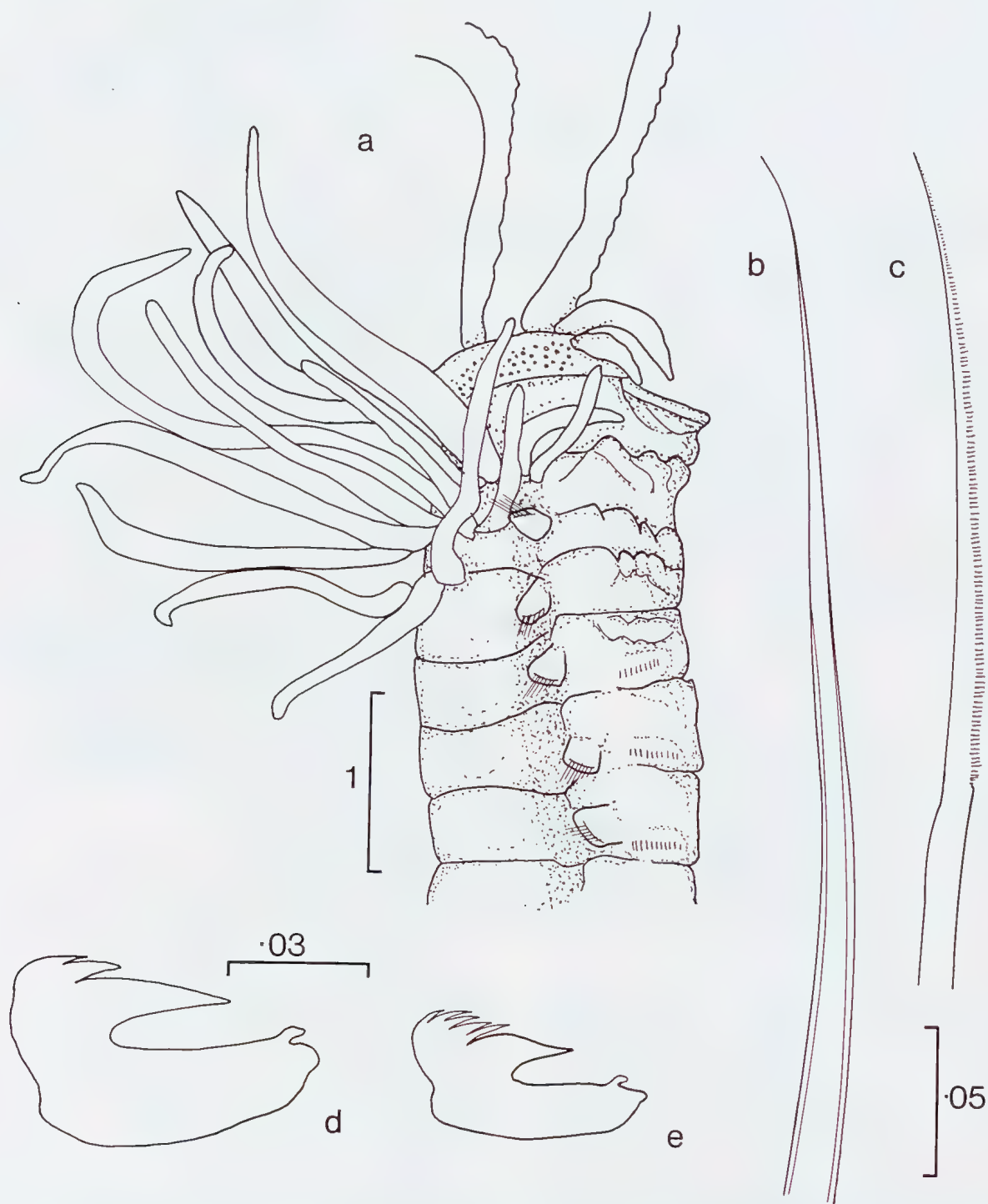


Fig. 2. *Euthelepus serratus* n.sp., holotype: a, head end, lateral view; b, c, two types of notosetae from setiger 10; d, anterior uncinus; e, posterior uncinus. All measurements in mm.

Euthelepus setubalensis McIntosh

Figs 1e-h; 4c

Euthelepus setubalensis McIntosh, 1885: 465-467, pl. L fig. 4; pl. XXVIII A fig. 13; Fauvel, 1927: 275-276; Amoureux, 1974: 146, 148, fig. 6.

Material examined. HOLOTYPE: collected off Setubal, Portugal (BMNH ZK 1885.12.1.358). Specimen in two pieces, anterior portion including head 3.2 mm long, 9 segments, 1.4 mm wide, posterior portion incomplete, 7.2 mm long, 10 segments, 1.4 mm wide.

Description. Body small, robust, anterior segments

short, well defined. Prostomium short, broadly U-shaped with shallow, transverse grooves on dorsal surface, ventrally forming longitudinally grooved upper lip, posteriorly produced as a marginally thickened, upturned tentacular ring. Buccal tentacles missing. Peristomium a complete ring dorsally, slightly longer than segment 2, ventrally forming lower lip, about 2x length of segment 2. Lateral lobes poorly developed, rounded, present on segments 2-4; slight lateral thickening on peristomium resembling a fourth lateral lobe (Fig. 1e).

Branchiae on segments 2-4 represented by long, thick,



Plate 1. Scanning electron microscope photographs of *Euthelepus serratus* n.sp. showing: **a**, tip of a long, nominally smooth type seta (x9,000); **b**, tip of a short serrated type seta (x9,000); **c**, as **a**, (1,100x); **d**, as **b**, (1,100x); **e**, notosetal fascicle from midbody showing two types of notosetae (200x); **f**, mid section of uncinal row from midbody (1,100x).

annulated, simple filaments, arising from anterior margin of segment, arranged as follows: segment 2, 1 + 1; segment 3, 1 + 1; segment 4, 1 + 1. Filaments on segments 2 and 4 displaced toward midline, with very small medial gap; filaments on segment 3 just dorsal to notosetae and separated by a large medial gap.

Notosetae are smooth, winged capillaries (Fig. 1f,g), extending from segment 3 for at least 17 segments; first 2 pairs with reduced notosetae, no notopodial lobes; subsequent pairs with small, dome-shaped notopodial lobes projecting from glandular pockets. Avicular uncini present from segment 5, arranged in straight rows on poorly developed, sessile tori. Uncini with elongate dorsal button, and well developed prow (Figs 1h; 4c); dental formula variable in one row as follows: MF:2:2:2:α. Nephridial papillae small, globular, present on posterior edge of segments 5–7 in line with top of uncinal row. Entire ventrum of first 9 segments glandular, discrete pads absent; posteriorly, anterior margin of segments with a narrow glandular strip connecting notopodia and neuropodia of one side with those of the other.

Comments. Many of the notosetae in the type specimen have damaged tips, but it appears that only smooth setae are present. Lateral lobes, although small, are present on segments 2–4. The only other Thelepiniae having lateral lobes are *Euthelepus kinsemboensis* and *E. serratus* n.sp. Both of these species may be distinguished from *E. setubalensis* in having serrated as well as smooth notosetae.

In the original description, McIntosh states that rudimentary bristle tufts (notosetae) are present on all three branchiferous segments (segments 2–4), but we could detect bristle tufts only on segments 3 and 4 in the type specimen. Similarly, Day (1963), on re-examining the type, found that notosetae began on segment 3. Caullery (1915), in a key to the Thelepiniae, states that notosetae start on segment 3 in *Euthelepus*, although we are unsure how he arrived at this conclusion or if he looked at the type species.

McIntosh believed that this genus could be distinguished from other genera within the Thelepiniae in regard to the structure and arrangement of the branchiae and the shape of the uncini, in particular the position and orientation of the attachment button. However, we feel that the shape and arrangement of branchiae is not a good generic character in the Thelepiniae, although it is a good specific character (Hutchings & Glasby, in press) and is probably related to the depth (see Discussion).

Habitat. Mud, calcareous sediment, 360–900 m.

Distribution. Atlantic Ocean, off Portugal.

Genus *Streblosoma* Sars

Streblosoma Sars, 1872 : 413.

Grymaea Malmgren, 1866 : 388. Not Fresenius, 1858 (Protozoa).

Eugrymaea Verrill, 1900 : 662.

Type species. *Grymaea bairdi* Malmgren, 1866.

Tentacular lobe short and compact, numerous buccal tentacles. Nil to 3 pairs of simple unbranched branchial filaments. Notoetae present from segment 2 (1st branchiferous) and continuing for a variable number of segments, setae smooth-tipped, capillaries. Uncini present from segment 5 (setiger 4).

Streblosoma atlanticus (Hartman & Fauchald)

new combination

Figs 3a; 4d

Euthelepus atlanticus Hartman & Fauchald, 1971: 172–174, pl. 29 figs a–d.

Material examined. HOLOTYPE (AHF Poly 0918): incomplete, 16 setigers, 8.1 mm long, 0.6 mm wide. PARATYPES: many (AHF Poly 0919) ranging from 11–25 mm long, 0.8–1 mm wide. All specimens collected from Station A73, 39°46.5'N 70°43.3'W north-west Atlantic.

Comments. The description given by Hartman & Fauchald, 1971 appears to be a composite description based on the paratypes. The holotype lies outside the size range given in the description and is also without a pygidium, yet a pygidium is mentioned in the description. Nevertheless, the holotype agrees with the description in all respects except one. A very small pair of notosetae consisting of only a few setae in each fascicle occurs on the first branchiferous segment (segment 2) arising just posterolaterally to the branchiae. The paratypes also appear to have notosetae from segment 2, although in the smallest animals the exact position of commencement could not be determined. The notosetae on segment 2 were overlooked by Hartman & Fauchald, who stated that the first pair occurs on the second branchiferous segment (segment 3).

In the holotype, notosetae are all smooth, winged capillaries (Fig. 3a). The first 2 setigers have no notopodial lobe, subsequent setigers to setiger 14 (the first of the longer, cylindrical segments mentioned by Hartman & Fauchald) have prominent, rectangular notopodial lobes; from setiger 14 the notopodial lobes are slightly reduced in size. Uncini start on segment 5 (setiger 3) as stated by Hartman & Fauchald. Dental formula for uncini on setiger 4 has the following range: MF:3–4:5–7:8–10:α. Uncini have a prominent up-turned dorsal button (Fig. 4d) and are arranged in short, slightly curved rows located immediately below the notopodia on sessile tori.

For comments as to why we are transferring this species to the genus *Streblosoma* see Discussion.

Habitat. Slope depths, 1330–1470 m.

Distribution. Known only from the north-west Atlantic.

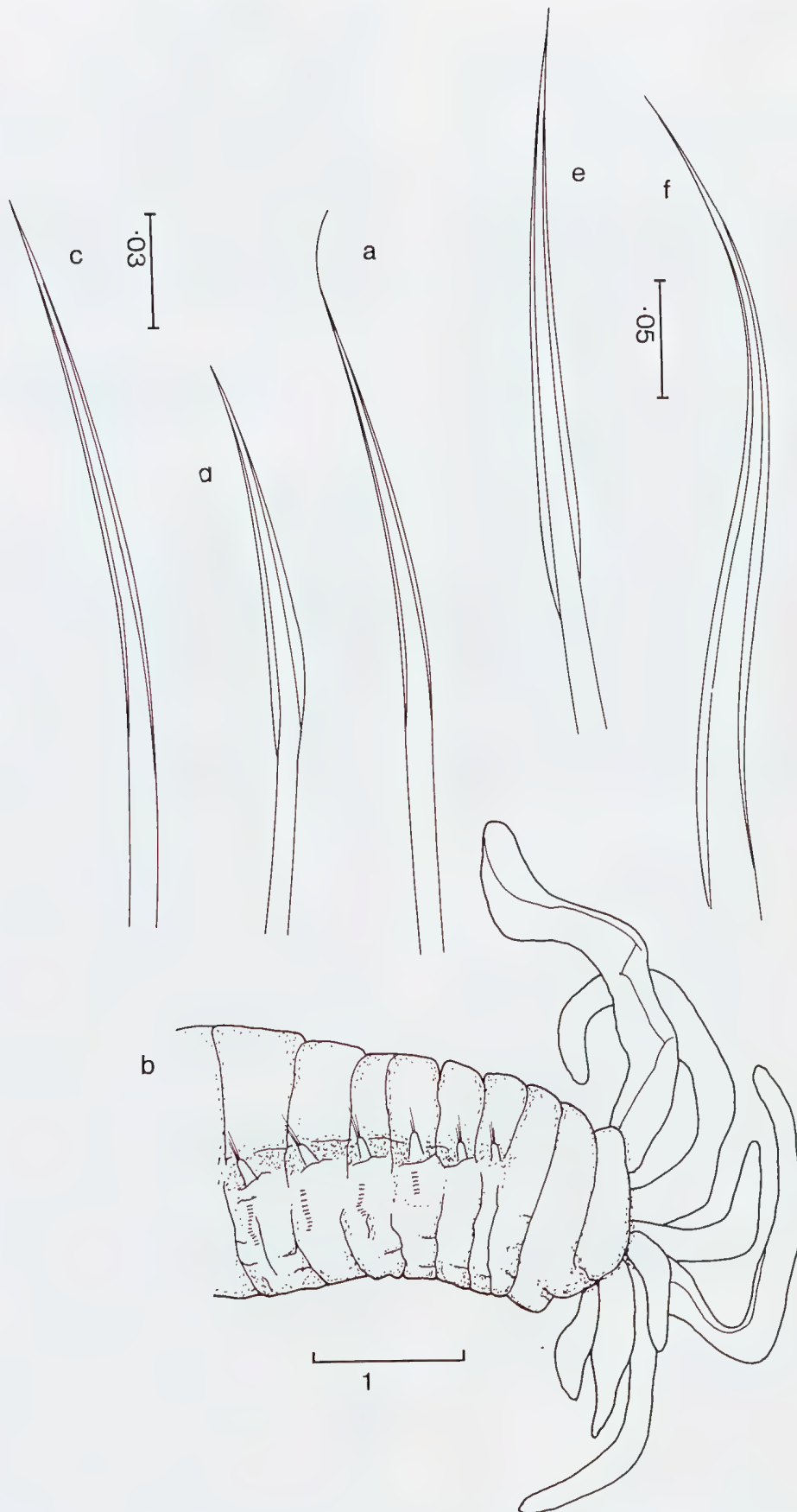


Fig. 3. *Streblosoma atlanticus*, paratype Poly 0919: **a**, notoseta from setiger 11. *Thelepus abbranchiatus*, paratype Poly 0921: **b**, head end, lateral view; **c**, **d**, two notosetae from setiger 12. *Thelepus malayensis*, holotype: **e**, **f**, two types of notosetae from setiger 7. All measurements in mm.

Streblosoma chilensis (McIntosh)

Fig. 4e

Euthelepus chilensis McIntosh, 1885: 467–468, pl. L1 figs 4, 5, pl. XXVIII A figs 14, 15.

Streblosoma chilensis.—Day, 1963: 370.

Material examined. LECTOTYPE (BMNH ZK 1885.12.1.359): incomplete, consists of two fragments, head end 16 setigers, 13.0 mm long, 2.3 mm wide, mid section 9 setigers, 9.0 mm long, 1.6 mm wide; branchiae and most tentacles detached, poor condition. PARALECTOTYPES 2 (BMNH ZK 1885.12.1.435): consist of two head ends, 14, 4 setigers, and 3 headless fragments; head ends range in width from 2.2–2.4 mm.

All material from Stn 299, 33°31'S 74°43'W off Valparaiso, Chile, 3950 m, grey mud, 14th December 1875, 'Challenger'.

Description. Lectotype with prostomium blunt-ended, flared into well defined tentacular ring. Buccal tentacles detached, with thick, very shallow food groove. Eyespots absent. Peristomium well developed, encircling prostomium, equal in length to segment 2. Lateral lobes absent. Branchiae detached, one pair on each of segments 2 and 3, indicated by branchial scars on anterior margins of segments, just above the notosetae.

Notosetae present as long, smooth, winged capillaries from segment 2, extending for at least 20 segments. Notopodial lobes short, rectangular for first few segments, thereafter reduced or absent. Neurosetae present as avicular uncini from segment 5, arranged in straight rows on poorly developed, sessile tori. Uncini with prominent, distally rounded, sub-terminal button and well developed rounded prow (Fig. 4e); dental formula of anterior uncinus: MF:1:3:2.

Nephridial papillae absent; coelomic gametes absent. Discrete glandular ventral pads absent, but ventrum glandular for first 10 segments.

Comments. The specimen designated as the lectotype here most closely resembles the diagrams of the head end in McIntosh's description, although his description appears to be based on all three type specimens. The paralectotypes are similarly in poor condition and closely resemble the lectotype. Day (1963) has transferred this species to the genus *Streblosoma* as the notosetae start on segment 2 and there are no lateral lobes, although he did not designate a lectotype. It clearly differs from the holotype of *Euthelepus setubalensis* in which notosetae start on segment 3 and lateral lobes, although small, are present on segments 2–4.

Habitat. Type specimens collected from blue mud in 3950 m. Day's (1963) specimen collected in 1240 m.

Distribution. Off Valparaiso, Chile; off west coast of Cape Town, South Africa.

Genus *Thelepus* Leuckart

Thelepus Leuckart 1849: 169.

Lumara Stimpson, 1854: 30.

Phenacia Quatrefages, 1865: 374.

Heterophenacia Quatrefages, 1865: 389.

Neottis Malmgren, 1866: 388.

Thelephusa Verrill, 1871: 6.

Thelepodopsis Sars, 1872: 414.

Protothelepus Verrill, 1900: 662.

Type species. *Amphitrite cincinnata* Fabricius, 1780.

Tentacular lobe short and collar like, usually with numerous eyespots. Branchiae consisting of numerous simple filaments arranged in transverse rows on segments 2–4. Notosetae from segment 3 (2nd branchiferous), continuing for numerous segments, consisting of smooth-tipped capillaries. Uncini from segment 5 (setiger 3) continuing for numerous segments.

Thelepus abbranchiatus (Hartman & Fauchald)

new combination

Figs 3b–d; 4f

Euthelepus abbranchiatus Hartman & Fauchald, 1971: 171–172, pl. 28 figs f–i.

Material examined. HOLOTYPE (AHF Poly 0920): nearly complete, about 80 segments, 27 mm long, 3 mm wide (max). PARATYPES 3 (AHF Poly 0921): one complete specimen about 76 segments, 23 mm long, 1.9 mm wide (max). Other specimens incomplete, 1.0–1.2 mm wide. All specimens collected from Stn Ch 103, 39°43.6'N 70°37.4'W, north-west Atlantic.

Comments. In their account of the species, Hartman & Fauchald (1971) state that the next two segments after the tentacular segment are setigerous, but in our examination of both the holotype and paratypes we found both post-tentacular segments to be asetigerous. The discrepancy would seem to be due to a typing error, as the two asetigerous segments are well defined and we do not believe they could be overlooked (Fig. 3b). The notosetae, then, are first present from segment 3.

Other important specific characters not mentioned in the original description of the holotype include the following: 30 pairs of smooth, winged notosetae (Fig. 3c,d); 50 pairs of uncini (Fig. 4f); small rectangular notopodial lobes throughout; and uncinal tori which are sessile on the thorax and occur as small, squared pinnules increasing in size posteriorly on the abdomen.

This species differs from the type species of *Euthelepus*, *E. setubalensis*, in the absence of branchiae and absence of lateral lobes. It appears more closely related to the abbranchiate *Thelepus* species which also have no lateral lobes and have notosetae from segment 3 and uncini from segment 5. For this reason it is transferred to the genus *Thelepus*.

There are three species of *Thelepus* recorded for which there are no, or only a few, minute branchial filaments present, viz. *T. abyssorum* Caullery, 1944, *T. paucibranchis* (Grube, 1878) and a new species of *Thelepus* described from Wollongong, Australia (Hutchings & Glasby, in press). *Thelepus abyssorum* most closely resembles *T. abbranchiatus* in the total absence of branchiae and in the number of pairs of notosetae and profile of the uncini. *Thelepus abyssorum*, however, has very long, narrow-winged

notosetae unlike the shorter, broader-winged notosetae of *T. abbranchiatus*.

The other two species differ from *T. abbranchiatus* in having a few minute branchiae. In addition, *T. paucibranchis* differs in the profile and dentition of the uncini, and the new species from Australia differs in having well defined eyespots and in the shape of the anterior uncini, which have no prow.

Habitat. Abyssal depths, 2022 m.

Distribution. Species known only from the type specimens collected off Nova Scotia, north-west Atlantic.

Thelepus malayensis (Caullery)
new combination
Figs 3e; 4g

Euthelepus malayensis Caullery, 1944: 182, fig. 146 A-F.

Material examined. HOLOTYPE (ZMA V pol 1765): Siboga expedition, Stn 52, 9°3'4"S 119°12'E, 960m; consisting of 3 fragments, probably incomplete, anterior fragment of 15 segments, 7.0 mm long; middle fragment 31 segments, 16 mm long; posterior fragment, including pygidium, 32 segments, 11 mm long; maximum width of all fragments 1.0 mm.

Description. Body long, slender, tapering very gradually from midbody; first 6 segments not well defined, next 7 well defined, moniliform, then becoming longer, cylindrical, finally decreasing in length near pygidium; middle segments with brown pigment bands

almost encircling body, but absent mid-dorsally and mid-ventrally.

Prostomium conical, produced posteriorly as short tentacular ring. Buccal tentacles slender, grooved, attached to anterior edge of tentacular ring. Eyespots absent. Peristomium smooth, about 2x length of segment 2. Lateral lobes absent.

Single branchia attached to posterior edge of segment 2 (the other branchia presumably missing) long, cylindrical, slightly tapered, extending back to about setiger 10. Segments 2 and 4 slightly elevated dorsally, segment 3 with prominent rounded dorsal crest on the anterior edge; dorsum over segments 2-4 slightly humped.

Notosetae consisting of smooth, winged capillaries of 2 lengths (Fig. 3e), present from segment 3, extending for at least 13 segments. Neurosetae present as avicular uncini, extending from segment 5 to near pygidium; arranged in single, short, straight to slightly curved rows throughout, decreasing in length after first few segments. Uncini with elongate, dorsal button and pointed prow (Fig. 4g); dental formula varying on setiger 10 as follows: MF:3:5-7:α. Uncini borne on slightly raised, glandular tori initially, becoming minute, squared, slightly elevated pinnules in middle and posterior segments.

Segments 4-13 with discrete ventral pads extending laterally to tori. Nephridial papillae absent.

Comments. Our interpretation of the arrangement of segments at the head end differs somewhat from

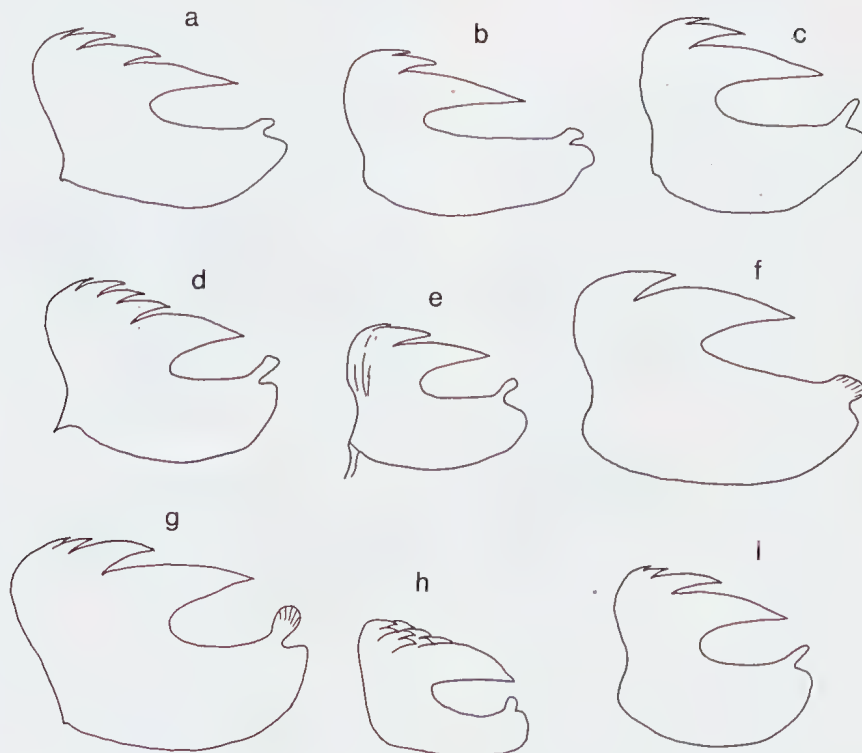


Fig. 4. A comparison of the shape of anterior uncini. a, *Euthelepus kinsemboensis*, holotype; b, *Euthelepus serratus* n.sp., holotype; c, *Euthelepus setubalensis*, holotype; d, *Streblsoma atlanticus*, paratype Poly 0919; e, *Streblsoma chilensis*, lectotype, drawn from McIntosh, 1885; f, *Thelepus abbranchiatus*, paratype Poly 0921; g, *Thelepus malayensis*, holotype; h, *Thelepus pascua*, holotype, drawn from Fauchald 1977a; i, *Thelepus tenuis*, holotype YPM No.2864. Uncini drawn to different scales.

Caullery's. Caullery (1944) states that the cephalic segment (segment 1) is very small, segment 2 is very long and has a pair of branchiae inserted on the extreme posterior edge, segment 3 is much shorter and segment 4 has the first pair of notosetae. We feel that Caullery's segment 2 consists of 2 segments—the peristomium (our segment 1) which forms the lower lip ventrally, and a shorter segment posteriorly (our segment 2). The branchiae, we believe, are attached to the posterior edge of this shorter segment.

Caullery states that the first notosetae appear on the second post-branchial segment. It is evident from his figures of the head end of the animal that he overlooked the small setal fascicle on the first post-branchial segment; the left side one is damaged and barely visible.

Thus, *T. malayensis* has notosetae from segment 3, uncini from segment 5, 1 pair of branchiae attached to segment 2 and no lateral lobes. In these last 2 respects it differs most notably from the type species of *Euthelepus* and we therefore transfer it to *Thelepus*. *Thelepus malayensis* thus differs from other species of *Thelepus* in having 0–1 pair of branchiae, in having very long, cylindrical branchial filaments and a prominent dorsal crest on segment 3.

Habitat. From 960 m.

Distribution. Known only from the type specimen collected off Sumbawa, Indonesia.

Thelepus pascua (Fauchald)

new combination

Fig. 4h

Euthelepus pascua Fauchald, 1977a: 57–58, fig. 12d–h.

Material examined. HOLOTYPE (USNM 53093): Galeta Reef, Panama, 17th March 1972; posteriorly incomplete, 29 setigers, 4.5 mm long, 0.75 mm wide.

Comments. Fauchald (1977a) states that the first notosetae occur on the third post-peristomial segment (segment 4) and that uncini (Fig. 4h) are present from the fourth setiger. We have re-examined the type specimen and found that a short row of uncini is also present on the third setiger.

The prostomium, we believe, forms a hood over the mouth and posteriorly forms a slightly raised tentacular ring on which a pair of tentacles is attached laterally. The peristomium is asetigerous, about 2 times length of the next segment, and forms the lower lip ventrally (see Fauchald 1977a, fig. 12d). The next segment (2) is asetigerous and has a pair of branchiae arising from the anterior margin. Segment 3 carries the first pair of notosetae and a single branchial filament (presumably one is missing) arising from the anterior margin.

The exact origin of the branchial filaments is very difficult to determine. Fauchald believes they arise from the posterior margin of the segments. Our interpretation of the origin of the branchiae, which differs from Fauchald's, and the arrangement of anterior segments

places the animal in the genus *Thelepus*. It does not belong to *Euthelepus* as no lateral lobes are present. Until more material can be examined and the segmental origins fully elucidated its relationship in the Thelepinæ is uncertain. *Thelepus pascua* differs from most other species of *Thelepus* in having only 2 pair of branchiae, the only other species with 2 pairs are *Thelepus cincinnatus* (Fabricius), *T. hamatus* Moore and *Thelepus vaughani* (Gravier). These three species have far more branchial filaments than *T. pascua* which has only a single pair of branchial filaments on each of segments 2 and 3.

Habitat. On reef in *Laurencia* zone.

Distribution. Known only from the holotype collected at Panama, Atlantic Ocean.

?*Thelepus tenuis* (Verrill)

Fig. 4i

Protothelepus tenuis Verrill, 1900: 662–663.

Euthelepus tenuis.—Caullery, 1915: 46–47.

Material examined. HOLOTYPE (YPM No.2864): Bermuda; a mounted specimen in very poor condition. *Thelepus tenuis* 1 (USNM 097587) from Hungry Bay, Bermuda, coll. M. Jones.

Description. The holotype consists of an anterior fragment of 16 setigers, approximately 5 mm long and 1 mm wide. Notosetae consisting of smooth, winged capillaries and uncini, commencing on the third setiger, each with an elongate, subterminal button and rounded prow becoming more pointed posteriorly (Fig. 4i). The remaining body is unrecognisable and essentially unidentifiable.

The material from Bermuda has two pairs of simple branchial filaments, first pair much larger than the second. Notosetae occur from the second branchiferous segment and extend for 22 segments. Uncini begin on setiger 3 and continue to the pygidium; they occur on slightly elongate tori on abdominal segments. The prostomium is glandular and ventrally forms a horseshoe shaped upper lip. The ventrum is glandular, but no distinct pads are present.

Comments. Caullery (1915) transferred this species to the genus *Euthelepus* on the basis of Verrill's description, although he did not examine the type. Caullery admits to having some difficulty in interpreting the numbering of the anterior segments from Verrill's description. As Verrill does not describe any lateral lobes, and, providing he did not overlook them, the species clearly does not belong to the genus *Euthelepus*. We questionably refer the species to *Thelepus* on the basis of the material examined from Bermuda which has notosetae beginning on the 2nd branchiferous segment.

Habitat. Unknown.

Distribution. Bermuda.

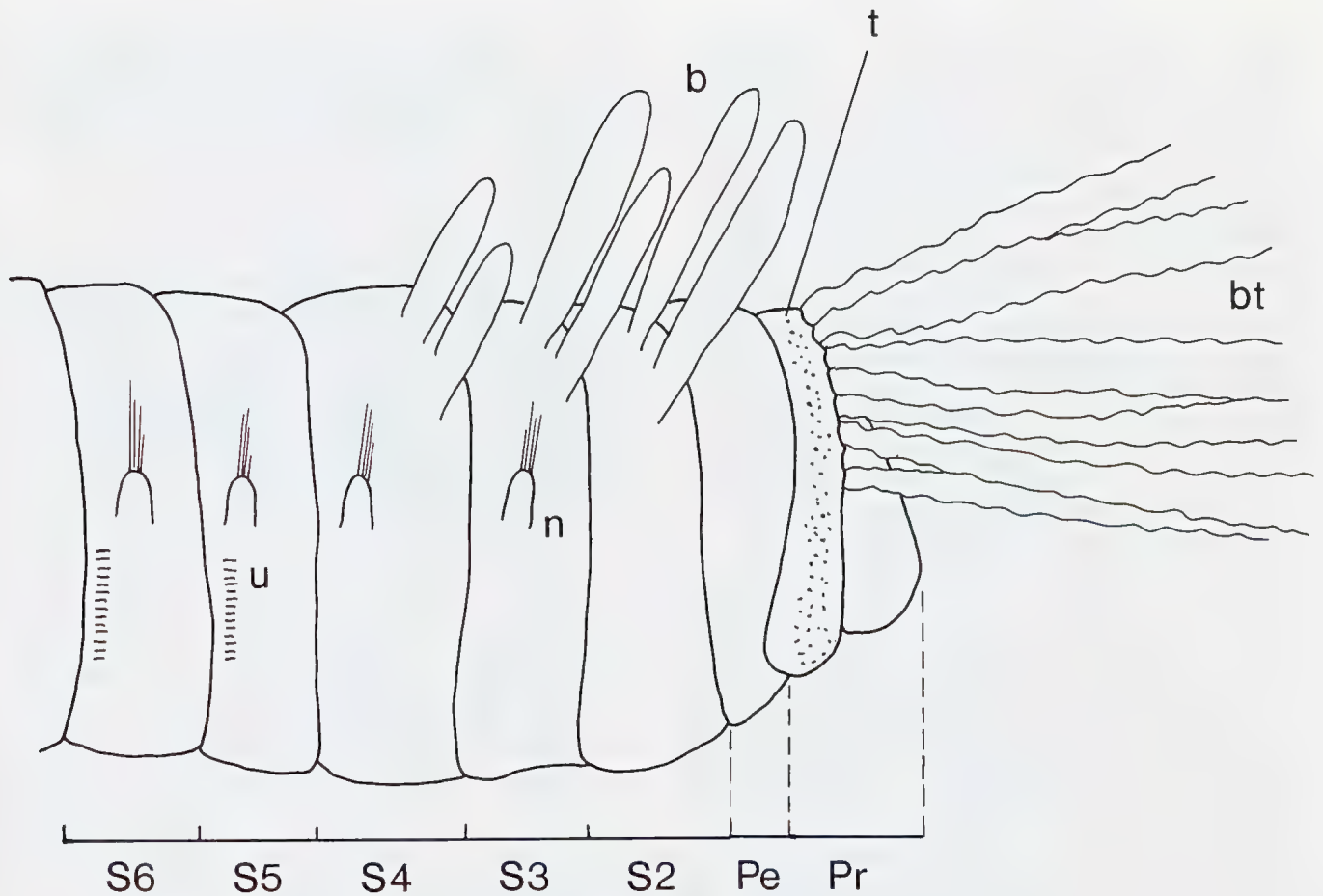


Fig. 5. An idealised Thelepinæ (*Thelepus*) showing terminology and numbering sequence of segments used in the text. Pr = prostomium; Pe = peristomium; S = setiger; bt = buccal tentacles; t = tentacular ring; b = branchiae; n = notosetae; u = uncini.

DISCUSSION

As there has been some confusion in the literature as to the exact terminology and numbering of anterior segments in Thelepinæ, the front end of an idealised Thelepinæ is illustrated in Fig. 5. This interpretation is based on adult morphology, as we have not had the opportunity to study the development of segments in larval and juvenile worms. Confusion with the terminology of numbering has led to two species with

notosetae beginning on segment 2, viz. *S. atlanticus* and *S. chilensis*, being transferred to *Streptosoma* (see Table 1). The segment on which both notosetae and neurosetae begin is a valid generic character and constant within a genus.

Of the remaining species originally described in *Euthelepus*, four species, viz. *T. abbranchiatus*, *T. malayensis*, *T. pascua* and *T. tenuis*, lack lateral lobes, and these have been transferred to the genus *Thelepus*. The remaining species all have lateral lobes on segments

Table 1. A comparison of some important generic characters in existing species of *Euthelepus* and their revised generic status.

Former status	Segment first appearance		Lateral lobes (segs)	Serrated notosetae	No. of branchial segments	Revised
	notosetae	uncini				
<i>E. kinsemboensis</i>	3	5	+(2-3,4?)	+	3	as former
<i>E. serratus</i> n.sp.	3	5	+(2-3)	+	3	—
<i>E. setubalensis</i>	3	5	+(2-4)	—	3	as former
<i>E. atlanticus</i>	2	5	—	—	2	<i>Streptosoma</i>
<i>E. chilensis</i>	2	5	—	—	2	transferred to
						<i>Streptosoma</i> by
						Day, 1963
<i>E. abbranchiatus</i>	3	5	—	—	0	<i>Thelepus</i>
<i>E. malayensis</i>	3	5	—	—	1	<i>Thelepus</i>
<i>E. pascua</i>	3	5	—	—	2	<i>Thelepus</i>
<i>E. tenuis</i>	3	5	—	?	2	<i>Thelepus</i>

+ present
— absent

2–3 or 2–4, although having noto- and neurosetae beginning on the same segments as *Thelepus*. The presence of lateral lobes is a valid generic character and we believe may indicate perhaps a common origin with *Thelepus*. A change in tube construction or environment in which they lived, selected for the development of glandular lateral lobes. We therefore believe that the development of glandular lateral lobes is an apomorphic character. Other data from the notosetae tend to support the common origin of the 2 genera. All *Thelepus* species examined both in this paper and by Hutchings & Glasby (in press) have smooth notosetae. However, some species of *Euthelepus* have both smooth and serrated notosetae (Figs 1b,c; 2b,c; Plate 1a–e). Examination of both types of setae under the SEM reveals that they are of a similar structure and that only the degree of separation of the chitin layers differs. We therefore reject Day's (1967) comments that *E. kinsemboensis* Augener be transferred to the genus *Amphitrite* because of the presence of serrated notosetae. The serrated notosetae of *Amphitrite* have a very different structure from those of *E. kinsemboensis*. The uncini of *E. kinsemboensis* have far more in common with members of the subfamily Thelepininae than with the subfamily Amphitritinae (see Fig. 4). Other genera of terebellids are characterised by serrated notosetae but we contend that they are of a very different structure from those in *Euthelepus*. We therefore are willing to include both serrated and smooth notosetae within a genus, admitting that serrated notosetae elsewhere are a useful generic character. Another character which we originally considered useful is the presence, in many of the species originally assigned to *Euthelepus*, of few branchiae which are long and thickened at the base, somewhat resembling ampharetid branchiae. However, all the species with this sort of branchiae are abyssal species and we suggest that this is an apomorphic character associated with an abyssal habitat rather than a generic feature.

At this stage, little can be said about the distribution of the genus *Euthelepus*: one is a deep-water species occurring off Portugal, and the new species occurs in shallow subtidal depths off the Australian coast. Probably several other species remain to be described and it may be that other recorded Thelepininae have been incorrectly identified because much of the material we examined in museum collections had been wrongly assigned to a genus. Also, if some species of the genus occur in deep water, this may explain the paucity of described species of the genus.

ACKNOWLEDGEMENTS. We would like to thank Australian Biological Resources Scheme for supporting this project and providing the salary for one of us (CG).

We would also like to thank the following people for sending us loans promptly and helping us in tracking down material. Ms Sue Williams (AHF), Dr David George and Mr Alex Muir (BMNH), Dr Gesa Hartmann-Schröder (HZM), Dr Kristian

Fauchald (USNM), Dr Seibrecht van der Spoel (ZMA), Mr Harold Feinberg (American Museum of Natural History, New York) and Dr W.D. Hartman (YPM). Finally, thanks to Ms June Adams for typing the manuscript.

References

- Amoureux, L., 1974. Annélides polychètes recueillies sur les pentes du talus continental au nord-ouest de l'Espagne et du Portugal (Campagne 1972 de la Thalassa'). Cuadernos de Ciencias Biológicas 3: 121–154.
- Augener, H., 1918. Polychaeta Beiträge zur Kenntnis des Meeresfauna West-Afrikas Herausgegeben von W. Michaelsen, Hamburg 2: 67–625.
- Caullery, M., 1915. Sur les Terebelliens de la Tribu des Thelepininae—Examen des genres. Tube spiral de *Streblosoma longiremis* n.sp. Bulletin de la Société Zoologique de France 40: 44–53.
- , 1944. Polychètes sédentaire de l'Expedition du SIBOGA : Ariciidae, Spionidae, Chaetopteridae, Chloraemidae, Opheliidae, Oweniidae, Sabellariidae, Sternaspidae, Amphictenidae, Ampharetidae, Terebellidae. Siboga Expedition Leiden 24(2): 1–204.
- Day, J.H., 1963. Polychaete fauna of South Africa. Part 7. Species from depths between 1000 and 3300 meters west of Capetown. Annals of the South African Museum 46: 353–371.
- , 1967. A monograph on the Polychaeta of southern Africa. Parts I and II, British Museum (Natural History) London, 878 pp.
- Fabricius, O., 1780. Fauna Groenlandica, systematice sistens, Animalia Groenlandica occidentalis, hactenus indagata quod nomen specificum triviale, vernaculumque; synonyma auctorum plurium, descriptionem, locum, victum, generationem, mores, usum, capturamque singuli, prout detegendi occasio fuit, maximaque parti secundum proprias observationes, Hafniae, pp. XVI+452.
- Fauchald, K., 1977a. Polychaetes from intertidal areas in Panama, with a review of previous shallow-water records. Smithsonian Contributions to Zoology 221: 1–81.
- , 1977b. The Polychaete Worms. Definitions and keys to the Orders, Families and Genera. Natural History Museum of Los Angeles County, Science Series 28: 1–188.
- Fauvel, P., 1927. Polychètes sédentaires. Addenda aux Errantes, Archiannélides, Myzostomaires. Faune de France 16: 1–494.
- , 1930. Annélides polychètes de Nouvelle-Calédonie recueillies par Mme A. Pruvot-Fol en 1928. Archives de Zoologie Expérimentale et Générale 69: 501–562.
- Gravier, C., 1906. Sur les annélides polychètes de la Mer Rouge (Térébelliens). Bulletin du Muséum National Histoire Naturelle, Paris 12: 451–454.
- Grube, A.E., 1878. Annulata Semperiana. Beiträge zur Kenntnis der Anneliden-fauna der Philippinen nach den von Herrn Prof Semper mitbrachten Sammlungen. Mémoires de l'Académie impériale des sciences de St Petersburg 25: pp.XI+300.
- Hartman, O., 1942. A review of the Types of polychaetous annelids at the Peabody Museum of Natural History, Yale University. Bulletin of The Bingham Oceanographic Collection, Peabody Museum of Natural History, Yale University Vol. III, Article 1.
- Hartman, O. & K. Fauchald, 1971. Deep-water benthic polychaetous annelids off New England to Bermuda and

- other North Atlantic areas. Part 2. Allan Hancock Monographs in Marine Biology 6: 1-327.
- Hutchings, P.A. & C.J. Glasby, in press. The Thelepinæ (F. Terebellidae) from Australia together with a discussion of the generic and specific characters of the subfamily. Proceedings of the Biological Society of Washington.
- Leuckart, R., 1849. Zur kenntnis der Fauna von Island. Archiv für naturgeschichte, Berlin 15.1 : 149-208, pl.3.
- Malmgren, A.J., 1866. Nordiska Hafs-Annulater Oefv. Forhandlingar Videnskabselskabet i Kristiania 22: 344-410.
- McIntosh, W.C., 1885. Report on the Annelida Polychaeta collected by H.M.S. Challenger' during the years 1873-76. Challenger Reports 12: 1-554.
- Moore, J.P., 1905. New species of Polychaetes from the north Pacific, chiefly from Alaskan waters. Proceedings of the Academy Natural Sciences Philadelphia 57: 525-554.
- Quatrefages, A. de, 1865. Histoire naturelle des Annelées marina et d'eau douce. Anélides et Gephyriens. Paris 1: 1-588.
- Sars, M., 1872. Diagnoser af nye Annelider fra Christiania-fjorden. Fördhandlinger, Videnskabselskabet i kristiania: 406-417.
- Stimpson, W., 1854. Synopsis of the marine Invertebrata of Grand Manan; or the region about the mouth of the Bay of Fundy, New Brunswick. Smithsonian Contributions to Knowledge 6: 1-67, pls 1-3.
- Verrill, A.E., 1871. Marine fauna of Eastport, Maine. Bulletin Essex Institute 3: 2-6.
- 1900. Additions to the Turbellaria, Nemertina and Annelida of the Bermudas, with revisions of some New England genera and species. Transactions Connecticut Academy of Arts and Sciences 10: 595-671.

Accepted 21 October 1985



***Codonocera cuspidata*, a New Species
of Pelagic Ostracode from off
Queensland, Australia
(Crustacea: Ostracoda: Cypridinidae)**

LOUIS S. KORNICKER

National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560, USA

ABSTRACT. *Codonocera cuspidata* is described and illustrated. The species was collected in a neuston tow north of Queensland, Australia, and is the second species of the genus reported from Australia. It differs from other species by a combination of characters of the 1st antenna, mandible, maxilla, 5th limb, 7th limb and Bellonci organ. A brief supplementary description of the type species of the genus *Codonocera cruenta* Brady, 1902, is presented, together with a key to *Codonocera* species in the *cruenta* group.

KORNICKER, LOUIS S., 1986. *Codonocera cuspidata*, a new species of pelagic ostracode from off Queensland, Australia (Crustacea: Ostracoda: Cypridinidae). Records of the Australian Museum 38(3): 119-134.

Members of the genus *Codonocera* are known only from Indo-Pacific and Australasian waters (McKenzie, 1967: 221). The genus has been recorded as far south as New Zealand (Barney, 1921: 178), but the only previous record in the vicinity of Australia is that of Bate & Sheppard (1982: 26), who identified 12 adult males from the Great Barrier Reef as *C. polygonia* Müller, 1906. Over 250 specimens of a new species of *Codonocera* captured in a neuston net north of Townsville, Queensland, provided the opportunity to study both the adult male and female as well as the A-1 and A-2 instars. The type species of the genus is briefly discussed.

***Codonocera* Brady**

Type species. *Codonocera cruenta* Brady, 1902: 188, pl. XXII, figs 1-10, by monotypy.

Distribution. Indo-Pacific and Australasian waters (McKenzie 1967: 221).

Poulsen (1962: 311) divided the genus into 2 informal groups: the *goniacantha* group and the *cruenta* group. The new species described herein is in the latter group.

Diagnosis of *cruenta* group. Mandible with a total of

6 claws and bristles on end joint. Maxilla: exopodite with 2 plumose bristles; 1st endopodial joint with 2 beta-bristles; 2nd endopodial joint with spines on a-bristles, and with a total of 7 b- and c-bristles. 5th limb: 2nd exopodial joint with 5 or 6 a-bristles, and with a total of 5 or 6 b'- and b"-bristles; outer branch of 3rd exopodial joint with 1 bristle much longer than other.

Discussion of type species. Through the courtesy of Mr P. S. Davis, Deputy Curator, the Hancock Museum, Newcastle upon Tyne, I received a slide (no. 1.54.15) containing appendages of the holotype of the type species, *Codonocera cruenta*. Unfortunately, details of many appendages are obscure but some characters are discernable. 1st antenna without spine on ventral margin of 1st joint. Longest end claw of mandible 46% length of 2nd endopodial joint; longest dorsal claw of end joint about 2/3 length of longest claw; shorter dorsal claw of end joint about 1/2 length of longest dorsal claw. Maxilla: 1st endopodial joint with 2 beta-bristles; end joint with spinous a-bristles, 7 b- + d-bristles, and posterior c-bristle with marginal spines. 5th limb: main tooth with 6 constituent teeth; outer lobe of 3rd exopodial joint with 1 long and 1 short bristle, but area obscure. Furca not distinct but probably with 3 claws

on each lamella as shown by Brady (1902: pl.12, fig. 7). Distribution of pigment: 1st antenna with elongate pink spot on distal part of 2nd joint dorsal to mid-height, and faint tint of pink dispersed throughout 3rd joint; 2nd antenna with small maroon spot near proximal end of protopodite near mid-height; mandible with small maroon spot near coxale endite, small maroon area near proximal ventral corner of basale; maxilla with 1 maroon spot near bases of 1st and 2nd endites; 5th limb with 1 small maroon spot proximal to main tooth of 1st exopodial joint; 6th limb with 6 diffuse spots of maroon tint dispersed throughout stem, and several diffuse spots in skirt; 7th limb without pigment; furca with many (about 10) maroon spots in area between girdle and lamellae, but apparently not within area covered by lamellae; copulatory appendage with proximal maroon spot; lateral eye without black pigment; medial eye and Bellonci organ not on slide.

Brady (1902: pl. XXII, figs 4,5) illustrated pigment spots on the mandible and 5th limb that agree in location with those on the present slide.

The appendages clearly indicate that the holotype of *C. cruenta* is in the *cruenta* group of Poulsen. It is less clear whether the specimens studied by Poulsen (1962: 319) were correctly identified as *C. cruenta*. The jaw of the 7th limb illustrated by Poulsen (1962: fig. 145j,k) is unlike that illustrated by Brady (1902: pl. XXII, fig. 6); unfortunately, the tip of the single 7th limb on Brady's slide is completely obscure. The 10 anteroventral grooves on the carapaces of the specimens identified by Poulsen were not mentioned in the descriptions of the species by either Brady or Müller (1906). In the present analysis I have assumed that Poulsen's identification of the species is correct. All known *Codonocera* species in the *cruenta* group are separated out in the accompanying key.

Key to species of *Codonocera* in the *cruenta* group

1. About 10 grooves present along anterior edge of shell below incisur and between list and shell margin, grooves perpendicular to shell edge. *C. cruenta*
 —Shell without 10 grooves. 2
2. Shell, triangular flap of infold of caudal process with medial spines; 5th limb, 1st exopodial joint with 5 constituent teeth. *C. weberi*
 —Shell, triangular flap of infold of caudal process without medial spines; 5th limb, 1st exopodial joint with 6 constituent teeth. 3
3. 1st antenna, 1st joint with ventral spine. *C. stellifera**
 —1st antenna, 1st joint without ventral spine. 4
4. 7th limb, middle tooth of comb twice length of shorter lateral teeth; tip of Bellonci organ blunt. *C. mortenseni*
 —7th limb, middle tooth of comb only slightly longer than lateral teeth; tip of Bellonci organ pointed. 5
5. Male 2nd antenna, broad proximal part of 3rd endopodial joint about 105% length of narrow distal part; maxilla, posterior c-bristle bare; 5th limb, 2nd exopodial joint with 5 a-bristles. *C. elongata*
 —Male 2nd antenna, broad proximal part of 3rd endopodial joint about 80% length of narrow distal part; maxilla, posterior c-bristle pectinate; 5th limb, 2nd exopodial joint with 6 a-bristles. *C. cuspidata*

**C. pusilla* Müller, 1906, and *C. penicillum* Müller, 1906 also fall here. They are insufficiently known to tell if they belong in the *cruenta* group.

Codonocera cuspidata n. sp.

Figs 1–9

Material examined. HOLOTYPE: AM P36127, adult female. PARATYPES: AM P36128, adult female; USNM 158594, 2 adult females; AM P36129, 2 adult females; AM P36130, P36131, 2 adult males; USNM 193157, 2 adult males; AM

P36132, 1 adult male; AM P36136, 1 A-1 male; AM P36137, 4 unsexed A-2 instars and P36250, 1 female A-2 instar; AM P36138, P36139, 2 A-1 females; P28852, 247 specimens (mostly A-1 instars, but some adult males and females and also A-2 instars); P36140, 1 A-2 male.

Type locality. North of Townsville, Queensland, Australia, 18°03'S, 147°10'E; 27 Feb. 1977; FNQ 79-105; neuston tow

No. 28; collected by The Australian Museum Fish Department and AIMS party on RV *Lady Basten*. Paratypes from same sample as holotype.

Etymology. From the Latin *cuspidatus* in reference to the cusps along the convex margins of shell ridges.

Description of male (Figs 1–5e). Carapace elongate with linear dorsal margin and broadly convex ventral margin; anterior of carapace broadly rounded dorsal to incisur but slightly concave immediately above inferior tip of rostrum; tip of rostrum with minute anterior projection; incisur short with broadly rounded posterior end; caudal process narrow in both lateral and dorsal views; dorsal edge of caudal process forming right angle with posterior edge of valve; when carapace closed, caudal process forming posteriorly oriented siphon; posterior edge of siphon in lateral view either linear or very slightly convex; dorsal edges of valves linear and slightly depressed; anterior half of dorsal margin slightly higher than posterior half resulting in slight step at mid-length (Fig. 1); anterior end of dorsal margin forming a fairly sharp corner on left valve but smoothly rounded on right; posterodorsal corner of each valve narrowly rounded in lateral view. Anterior margin below incisur without grooves perpendicular to valve edge.

SURFACE ORNAMENTATION. Narrow ridge along dorsal edge of incisur dividing into 2 branches at dorsal inner corner of incisur (1 branch continuing along ventral margin of incisur; 2nd branch continuing ventrally and anteriorly and intersecting anterior edge of valve just ventral to incisur) (Fig. 1). Surface of valves with abundant crescent-shaped ridges convex posteriorly; posterior margin of ridges cusped and forming high angle with valve surface. Long hairs forming vertical row near posterior end of each valve, and also present along posterior half of dorsal margin of each valve (Fig. 1); shorter hairs sparsely distributed over valve surface.

INFOLD (Fig. 2a,b). Rostral infold with 14 bristles forming row on left valve of AM P36130, and only 6 on right valve (probably aberrant); 1 long bristle posterior to row; 2 small bristles at inner end of incisur,

and 2 unequal bristles on dorsal edge of incisur; anteroventral infold with 1 bristle near inner edge of infold close to incisur, then 21 bristles forming row extending to mid-length of ventral margin; list along ventral margin broadening near caudal process forming triangular flap just anterior to caudal process; flap bearing bristles along edge and with pores present on lower half; list crenulate posterior to anteroventral bristles of left valve only.

CENTRAL ADDUCTOR MUSCLE ATTACHMENTS (Fig. 1). Consisting of 2 vertical rows of elongate attachments (3 in anterior row, 4 in posterior row); 3 round attachments forming vertical row between the rows of elongate attachments; the upper 2 round attachments smaller than the lower round attachment; 2 closely spaced round attachments dorsal to other scars. An additional round attachment present dorsal and posterior to other 5, at about mid-height of valve (not shown in Fig. 1).

SERVAGE. Lamellar prolongation (with smooth outer edge) broadest in vicinity of incisur; servage divided into dorsal and ventral segments at incisur; lamellar prolongation absent along posterior edge of caudal process.

PIGMENTATION. Lavender colouration within haemocoel forming stellate patterns visible through shell; stellate patterns faint in some specimens.

SIZE (length x height). AM P36130, 2.89 x 1.89 mm; AM P36131, 2.99 x 1.87 mm; USNM 193157, AM P36132, 3 specimens, 2.87 x 1.89 mm, 2.92 mm x 1.97 mm, 2.83 x 1.92 mm.

FIRST ANTENNA (Fig. 2c–e). 1st joint bare. 2nd and 3rd joints with lavender pigment; 2nd joint with abundant spines on medial surface and along ventral margin; 3rd joint short, with 2 bristles bearing short marginal spines (1 dorsal bristle close to 2nd joint, and 1 ventral terminal bristle). 4th joint with 2 terminal bristles bearing short marginal spines (1 ventral, 1 dorsal). Sensory bristle of 5th joint with about 20 long filaments near middle on broad proximal part of bristle, and 4 shorter and more slender filaments on slender distal part of bristle. Medial bristle of 6th joint slender with short marginal spines, about twice length of fused joints 7 and 8. 7th joint: a-bristle with short marginal spines, about same length as bristle of 6th joint, but twice its width; b-bristle about 3 times length of a-bristle, with short, bare filament proximal to bulbous part of bristle, then a long filament terminating in bouquet comprising 5–10 suckers and 1 short stem without sucker; 3 short filaments present on b-bristle distal to bouquet; c-bristle almost twice length of b-bristle, with short proximal filament proximal to bulbous part of bristle, then a long stout filament terminating in bouquet comprising 5–6 suckers and 1 short stem without sucker; 8 slender filaments present distal to bouquet; suckers of c-bristle slightly farther from tip of limb than suckers of b-bristle. 8th joint: d- and e-bristles about same length as b-bristle, bare with blunt tips; f- and g-bristles 6 times length of b-bristle, with many short marginal filaments; g-bristle slightly longer than f-bristle.

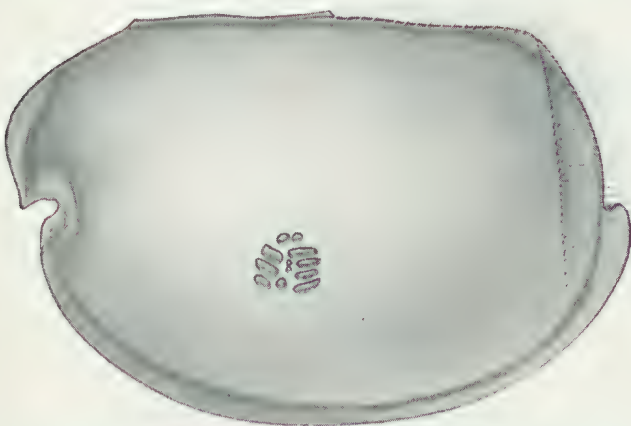


Fig. 1. *Codonocera cuspidata*, adult male paratype from left side [AM P36130], length 2.89 mm (stellate pigmentation not shown).



Fig. 2. *Codonocera cuspidata*, adult male paratype [AM P36130]: a, rostrum of left valve from inside (all bristles not shown); b, caudal process of left valve from inside; c, left 1st antenna (all long filaments of sensory bristle of 5th joint and all suckers of b- and c-bristles not shown); d, suckers of b-bristle; e, suckers of c-bristle; f, endopodite of right 2nd antenna; g, upper lip from left side.

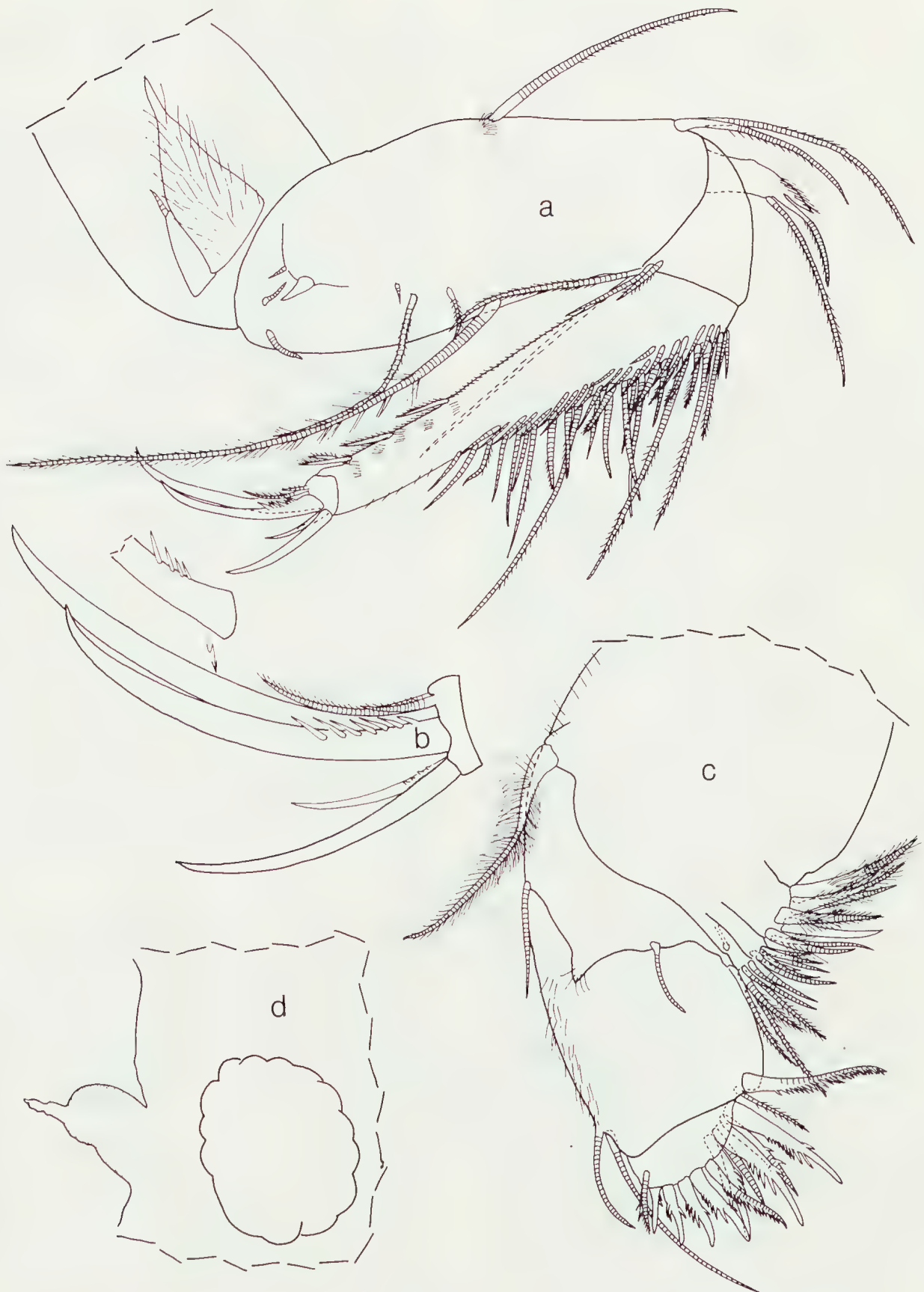


Fig. 3. *Codonocera cuspidata*, adult male paratype [AM P36130]: **a**, left mandible; **b**, detail of claws and bristles of end joint (proximal ventral spines on longest claw not shown); **c**, right maxilla (exopodite not shown); **d**, medial eye, Bellonci organ, and outline of left lateral eye.

SECOND ANTENNA. Medial bristle of protopodite with short marginal spines, about same length as distal bristle of 1st endopodial joint. Endopodite 3-jointed (Fig. 2f): 1st joint cylindrical with 1 long and 3 short proximal bristles and 1 long distal bristle; the long proximal bristle and the distal bristle with short marginal spines; 2nd joint broadening distally, with 2 pectinate marginal bristles, and 4 small rounded teeth lateral to bristles; 3rd joint reflexed on 2nd with rounded corner, about 12 nodes (proximal 8 closely spaced) along proximal outer edge, about 20 serrations along distal inner edge, minute spines forming rows in vicinity of serrations (spines not shown on illustrated limb), and 2 pointed teeth at tip. Exopodite: ventral margin of bristle of 2nd joint with 14 stout rounded teeth followed by 7 smaller, slender spines; dorsal margin of bristle with 3 minute teeth; terminal segment of bristle about same length as combined lengths of segments with slender spines; bristles of joints 3–8 with natatory hairs, no spines; 9th joint with 1 short and 3 long bristles, all with natatory hairs, no spines; basal spines small; lateral spine of 9th joint obscure on specimen examined.

MANDIBLE (Fig. 3a,b). Coxale endite, coxale, basale and 1st endopodial joint with lavender pigment. Coxale endite stout, hirsute, with tip bearing 1–2 stout spines, and with small basal bristle. Basale with 3 a-bristles (2 proximal, 1 distal), a short stout spine near proximal a-bristle, a minute b-bristle near proximal c-bristle, and 3 c- and d-bristles (the longest and most distal with wreaths of long spines); dorsal margin of basale with bare mid-bristle just reaching past end of joint, and 2 terminal bristles (lateral of these with short marginal hairs; medial bristle about $\frac{3}{4}$ length of lateral bristle, with stouter spines on proximal half). Exopodite about $\frac{2}{3}$ length of dorsal margin of 1st endopodial joint, hirsute along margin; distal bristle reaching just past middle of proximal bristle, both with short marginal spines. 1st endopodial joint with 4 ventral bristles (1 minute, 1 about $\frac{2}{3}$ length of dorsal margin of joint, and 2 reaching past middle of ventral margin of 2nd endopodial joint, all bristles with short marginal spines). 2nd endopodial joint: medial surface and ventral margin spinous; ventral margin with 4 slender pointed bristles forming groups of 1, 1, and 2 bristles, all with spines along ventral margin; bristles in distal pair same width and length as others; dorsal margin of 2nd joint with about 15 short, medium and long bristles (1 long bristle near mid-length with base on lateral side), bare or with short, faint, marginal hairs, and about 25 faint knife-like bristles with bases on medial surface and forming rows, and about 7 bristles with stout distal spines. End joint with 4 claws and 2 bristles (Fig. 3b); longest lateral claw 44–47% length of 2nd endopodial joint (length of claw determined by measuring length of straight line connecting ends of arc formed by curved claw; length of 2nd endopodial joint measured along middle of joint), and with 4–5 proximal marginal spines; medial claw only slightly smaller than lateral and with 7 proximal spines; medial dorsal claw about $\frac{1}{2}$ length longest claw and without spines; lateral dorsal claw

about $\frac{1}{3}$ length of longest claw and with 4 faint proximal spines; lateral ventral bristle about same length as lateral dorsal claw, with short spines along ventral margin; medial bristle about $\frac{1}{2}$ length of lateral bristle, with short marginal spines.

MAXILLA (Figs 3c; 4a,b). Precoxae and coxae with fringe of dorsal hairs. Endites with lavender pigment; endite I with 7 spinous and pectinate bristles; endite II with about 7 spinous and pectinate bristles; endite III with about 5 spinous and pectinate terminal bristles and 1 spinous bristle near base of exopodite, and with small glandular protuberance on anterodistal margin (Fig. 3c). Coxale with long, stout, plumose dorsal bristle. Basale with 1 short, bare, dorsal bristle, 1 short, bare medial bristle near ventral margin, and 1 long, stout, spinous, ventral bristle. Exopodite well developed, hirsute, with 3 bristles (proximal outer bristle plumose and with base close to terminal bristles, terminal outer bristle plumose, inner terminal bristle with short marginal spines). 1st endopodial joint with hairs along dorsal margin, with 2 slender alpha-bristles with short, faint, marginal spines, and 2 beta-bristles (outer bristle long, stout, pectinate; inner bristle about $\frac{2}{3}$ length of outer bristle, narrow, ringed, with short marginal spines); cutting tooth well developed, with 2 cusps. End joint with 3 stout, pectinate a-bristles (each bristle with distal spine on each margin stouter than others, and with part of bristle distal to large spines slender, bare, ringed [Fig. 4b]; outer a-bristle with 5 spines along anterior edge and 3 on posterior edge; middle a-bristle with 7 spines along anterior edge and 3 along posterior edge; inner a-bristle with 13 spines along anterior edge and 2 spines along posterior edge); 5 stout, unringed, b-bristles (anterior bristle short, triangular, with or without 1 marginal spine; remaining bristles with 3–7 stout marginal spines); 2 pectinate c-bristles (anterior bristle with base medial to anterior b-bristle and with slender marginal spines, posterior bristle with base medial to inner d-bristle and pectinate); and 3 pectinate d-bristles with 7–10 marginal spines.

FIFTH LIMB (Fig. 4c–f). Epipodial appendage with 61 bristles; protopodite with small rounded anterior tooth. Endite I with 5 spinous bristles; endite II with 5 bristles (1 small, bare, 4 spinous and pectinate); endite III with 6–7 bristles (1 small, bare, others spinous and pectinate). Exopodite: anterior side of 1st joint with 3 anterior bristles (outer bristle with long proximal hairs and short distal spines; inner paired bristles comprising 1 long stout bristle with a few spines, and 1 slender bristle about half length other bristle, with long proximal and short distal spines); main tooth comprising small bare peg and 6 constituent teeth (posterior tooth small with 1 faint marginal tooth; anterior tooth long, stout, with 2 small proximal teeth; remaining teeth with several marginal teeth; bristle proximal to peg with faint marginal spines; 2nd joint with 6 stout pectinate a-bristles (longest of these with 9 teeth), 6 b' + b''-bristles (longest of these with 14 marginal teeth), 1 posterior c-bristle with long proximal hairs and short distal spines, and 1 anterior d-bristle with abundant long proximal



Fig. 4. *Codonocera cuspidata*, adult male paratype [AM P36130]: **a**, detail of right maxilla showing alpha-bristles (unlettered) of 1st endopodial joint, and b- and d-bristles of end joint; **b**, detail of left maxilla showing beta-bristles (unlettered) and cutting tooth of 1st endopodial joint, and a- and c-bristles of end joint; **c**, detail of right 5th limb from anterior showing anterior bristles of 1st exopodial joint and d-bristle of 2nd exopodial joint; **d**, detail of left 5th limb from posterior showing main tooth and proximal bristle of 1st exopodial joint, and a-bristles of 2nd exopodial joint; **e**, detail of left 5th limb from posterior showing b'- and b''-bristles of 2nd exopodial joint; **f**, detail of left 5th limb from posterior showing bristles of exopodial joints 3-5.



Fig. 5. *Codonocera cuspidata*, adult male paratype [AM P36130]: **a**, left 6th limb; **b**, 7th limb; **c**, Detail from **b**; **d**, tip of opposite 7th limb; **e**, posterior of body from left side showing proximal part of 7th limb, left furcal lamella, left copulatory apparatus, left Y-sclerite (dashed) and other sclerotized parts (stippled). Adult female holotype [AM P36127]: **f**, caudal process of right valve from inside; **g**, endopodite of right 2nd antenna; **h**, medial eye, Bellonci organ and outline of right lateral eye.

hairs and small distal spines; inner lobe of 3rd joint with short proximal bristle with long proximal hairs and short distal spines, and long distal bristle with short marginal spines; outer lobe of 3rd joint with short proximal bristle and longer terminal bristle, both with short marginal spines; 4th and 5th joints fused, with 3 bristles, all with short marginal spines; outer lobe of 3rd joint and fused 4th and 5th joints hirsute. Distal parts of endites and exopodial joints with lavender pigment.

SIXTH LIMB (Fig. 5a). Limb with lavender pigment; 4–5 bristles in place of epipodial appendage; endite I with 3 bristles (1 long terminal, 2 short, medial); endite II with 1 or 2 short medial bristles and 2 terminal (1 long, 1 short); endite III with 1 short medial bristle and 2 terminal bristles (1 long, 1 short); endite IV with 4 bristles; end joint hirsute, with 32–34 bristles (posterior 2 plumose, others with long proximal and short distal spines, or only short spines); with exception of 2 plumose posterior bristles, bristles of posterior half of end joint with bases medial and proximal to ventral margin of joint.

SEVENTH LIMB (Fig. 5b–d). Each limb with 6 proximal bristles (3 + 3) and 6 distal (3 + 3); each bristle with 3–7 terminal bells. End comb with central curved tooth not much longer than 4 teeth on each side (latter teeth with marginal spines). Jaw opposite comb with 3 teeth bearing marginal spines.

FURCA (Fig. 5e). Lavender pigment in lamellae proximal to claws; claw 1 of right lamella anterior to that of left; each lamella with 4 claws decreasing in size posteriorly along lamella; each claw with lateral and medial row of small teeth along posterior margins; teeth absent near tip of claw; claws 1–3 with abundant short hairs along anterior margin; minute spines forming rows just posterior, and also proximal, to base of claw 4; anterior margins of both lamellae with short hairs forming rows.

BELLONCI ORGAN (Fig. 3d). Small, finger-like, with pointed tip.

EYES (Fig. 3d). Medial eye bare, with small area with brown pigment. Lateral eye large, with black pigment and about 27 ommatidia (exact number uncertain).

POSTERIOR OF BODY (Fig. 5e). Abundant hairs forming narrow transverse row on margin in vicinity of posterior muscle attachment and posterior to end of Y-sclerite; hairs absent elsewhere.

Y-SCLERITE (Fig. 5e). Typical for Cypridininae.

COPULATORY LIMBS (Fig. 5e). Fairly small, lobate, with minute bristles; tubular vas deferens long, S-shaped, entering anterodorsal corner of testes.

UPPER LIP (Fig. 2g). Unpaired anterior part and paired posterior part with fairly large glandular openings; each paired part with 2 small tusks (anterior of these lateral, other with base in same plane as paired lobe but posterior to it; each tusk with only 2–3 glandular openings; glandular field containing about 7 small indistinct glandular openings present rather high on lip, proximal to each pair of tusks; posterior part of lobes hirsute.

Description of female (Figs 5f–8). Carapace higher

relative to length than carapace of male, and also larger (Fig. 6); dorsal margin convex, but fairly linear in central part; anterior end of dorsal margin forming slight hump on left valve but not on right; posterodorsal corner of each valve rounded; posterior end of caudal process fairly linear (Fig. 5f); incisur and anterior margin of carapace similar to that of male; caudal process of each valve forming half of posteriorly oriented siphon (Fig. 7f).

SURFACE ORNAMENTATION. Narrow crenulate ridge along dorsal margin of incisur continuing ventrally and intersecting edge of valve ventral to incisur (Fig. 7c,d); surface of valves with abundant crescent-shaped ridges (Figs 7–8c). Several long hairs forming irregular vertical row near posterior end of each valve; short hairs sparsely distributed over valve surface and emerging from open pore having raised rim and single node (Fig. 8c).

INFOLD (Figs 5f; 8d–f). Rostral infold with 14–17 divided bristles forming outer row and 1 bristle near middle; 2 minute bristles at inner end of incisur, and 2 unequal bristles on dorsal edge of incisur; anteroventral infold with 1 small bristle close to incisur, then 24–27 bristles forming row extending to mid-length of ventral margin; list along ventral margin broadening near caudal process forming triangular flap bearing small bristles along outer edge, and also with numerous minute pores (about 30); ventral list posterior to anteroventral bristles crenulate on left valve only.

CENTRAL ADDUCTOR MUSCLE ATTACHMENTS. Similar to those of male.

SERVAGE (Figs 5f; 8e,f). Lamellar prolongation with smooth outer edge broadest in vicinity of incisur, dividing into dorsal and ventral segments at incisur, but absent along posterior edge of caudal process. Another lamellar prolongation present along posterior edge of triangular flap of infold in vicinity of caudal process; prolongation divided at posterior tip of triangular process (Fig. 5f).

PIGMENTATION. Similar to that of male.

SIZE (length x height). Holotype, AM P36127, 3.22

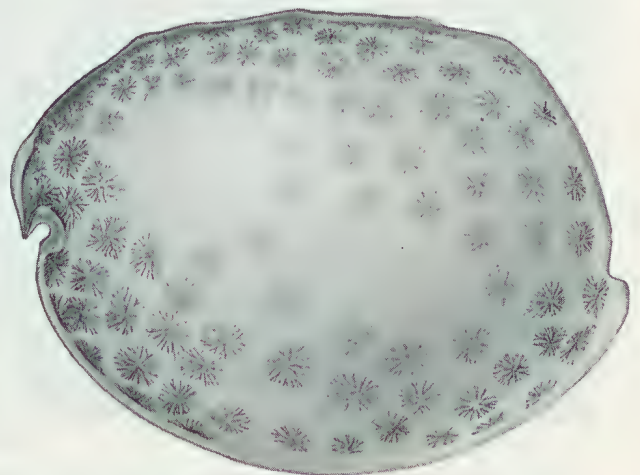


Fig. 6. *Codonocera cuspidata*, adult female holotype [AM P36127] from left side, length 3.22 mm.

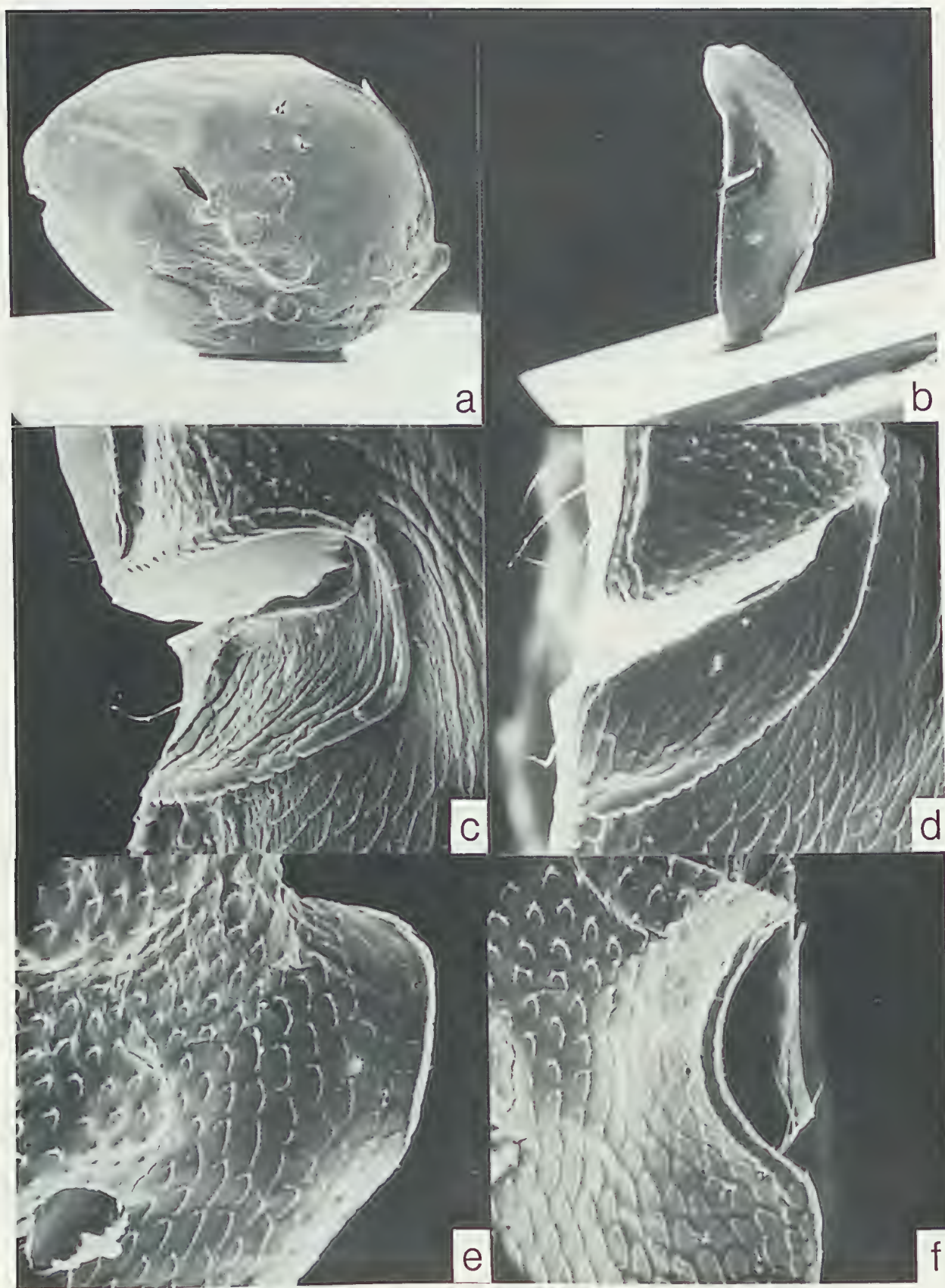


Fig. 7. *Codonocera cuspidata*, adult female holotype [AM P36127], left valve, length 3.22 mm: a, outside, X 32; b, anterior, X 31; c, incisur from left, X 250; d, incisur from anterior, X 250; e, caudal process from left, X 300; f, tip of caudal process from posterior, X 300. (Micrographs reduced to 80% for publication.)

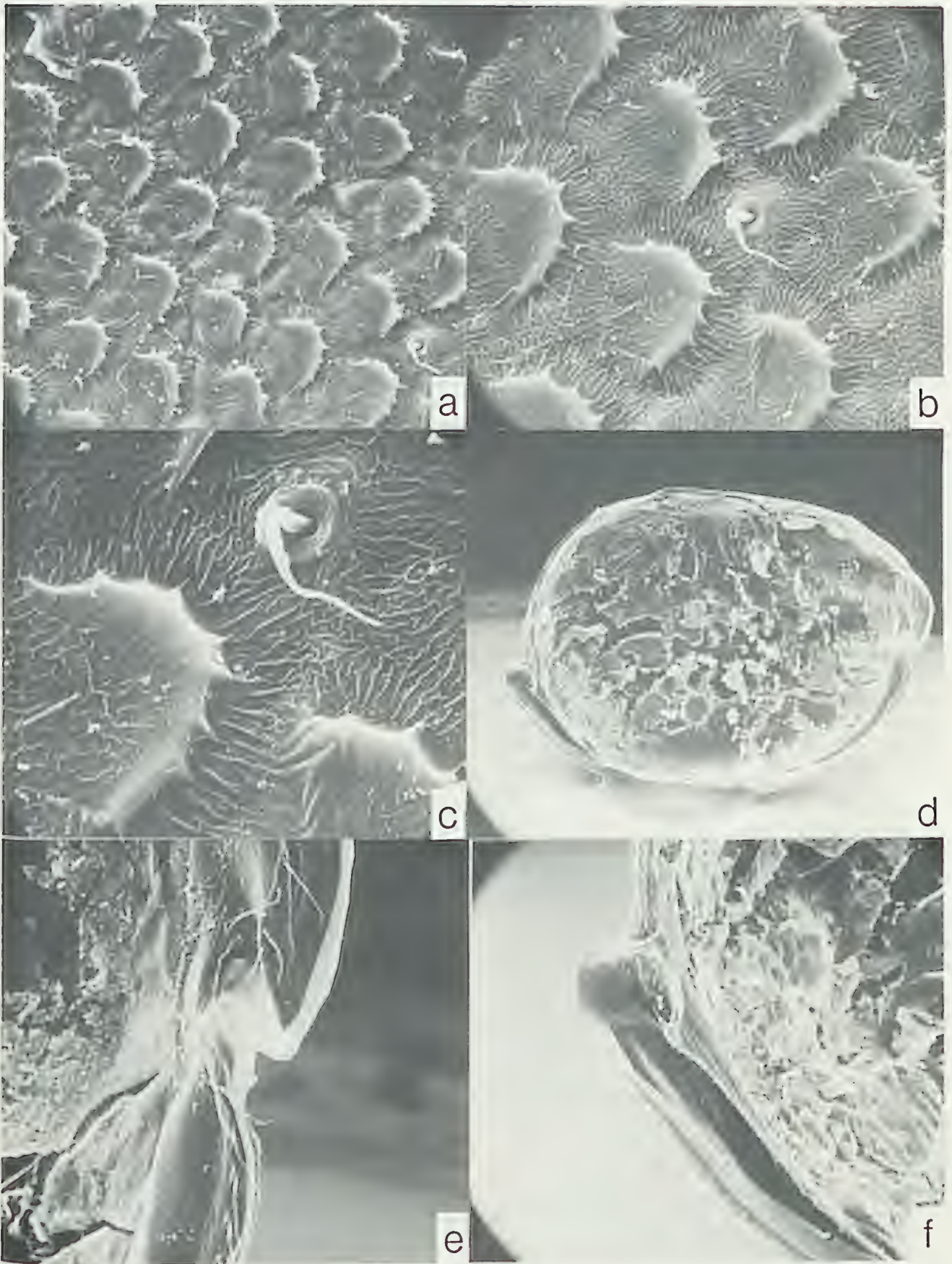


Fig. 8. *Codonocera cuspidata*, adult female holotype [AM P36127], left valve: a, cusped ridges near valve mid-length; b, detail from lower right of "a", X 1500; c, detail of bristle in "b", X 3000; d, inside of valve, X 30; e, incisor from inside, X 150; f, caudal process from inside, X 110. (Micrographs reduced to 80% for publication.)

x 2.40 mm; AM P36128, 3.44 x 2.54 mm; USNM 158594, AM P36129, 4 specimens, 3.13 x 2.48 mm, 3.43 x 2.60 mm, 3.45 x 2.58 mm, 3.45 x 2.61 mm.

FIRST ANTENNA. Joints 1–4 similar to those of male. Sensory bristle of 5th joint with 9–10 long filaments on broad proximal part of bristle, and 4 shorter and more slender filaments on slender distal part of bristle. Medial bristle of 6th joint similar to that of male. 7th joint: a-bristle similar to that of male; b-bristle about 3 times length of a-bristle, with 5 short marginal filaments; c-bristle broken on both limbs of specimen examined, stout, with short filaments on remaining part. 8th joint: d- and e-bristles similar to those on male; f-bristle about 3 times length of b-bristle, with 9 slender marginal filaments; g-bristle about 5 times length of b-bristle, with about 14 slender marginal filaments (distal marginal filament minute).

SECOND ANTENNA. Protopodite similar to that of male. Endopodite 3-jointed (Fig. 5g): 1st joint with 1 long and 2–3 small proximal bristles and 1 long distal bristle; 2nd joint about same length as 1st, bare; 3rd joint about half length of 2nd, with long terminal bristle about $\frac{1}{3}$ longer than endopodite. Exopodite: ventral margin of bristle of 2nd joint with 14 stout rounded teeth followed by 1 pointed spine; dorsal margin of bristle with 14 small, slender spines (base of each spine opposite base of tooth or spine of ventral margin); tip of bristle bare except for minute spine at tip. Basal spines on joints 5–8; some spines with minute, distal, marginal spine at each side near base of broad, pointed tip; lateral spine of 9th joint also with marginal spines but with rounded tip, about half length of 9th joint; exopodite otherwise similar to that of male.

MANDIBLE. Coxale, coxale endite, basale, all with lavender pigment; longest lateral claw of 3rd endopodial joint 40–44% of length of 2nd endopodial joint; limb otherwise similar to that of male.

MAXILLA. Endites I–III with 6, 6, 5 bristles; limb otherwise similar to that of male.

FIFTH LIMB. Small posterior tooth of main tooth of 1st exopodial joint with 4–5 marginal teeth. 2nd exopodial joint: longest a-bristle with 8 marginal teeth; longest of b'- + b"-bristles with 16 marginal teeth (proximal 2 of these minute). Limb otherwise similar to that of male.

SIXTH LIMB. 4 bristles in place of epipodial appendage; endite II with 2–3 short medial bristles and 2 terminal bristles (1 long, 1 short); endite III with no or 1 short medial bristle and 2 terminal bristles (1 long, 1 short); end joint with 26–28 bristles (posterior 2 plumose, others with long proximal and short distal spines, or only short spines). Limb otherwise similar to that of male.

SEVENTH LIMB, FURCA, BELLONCI ORGAN (Fig. 5h), EYES (Fig. 5h), POSTERIOR OF BODY, Y-SCLERITE, UPPER LIP. Similar to those of male.

GENITALIA. Small oval with attached ovoid spermatophore on each side of P36127.

Description of A-2 male (instar IV) (Fig. 9a,b). Carapace with convex dorsal and ventral margins (Fig.

9a); rostrum and caudal process similar to those of adult female; dorsal margin with linear part terminating posteriorly at midlength and forming slight step; small angular corner at anterior end of dorsal margin of left valve only. Anterior margin below incisur without grooves perpendicular to valve edge.

SURFACE ORNAMENTATION. Similar to that of adult.

INFOLD. Not examined.

CENTRAL ADDUCTOR MUSCLE ATTACHMENTS, SELVAGE: Similar to those of adult.

PIGMENTATION. Carapace pink, especially along edges, but without stellate chromatophores.

SIZE: AM P36140, length 1.83 mm, height 1.32 mm.

FIRST ANTENNA. 1st joint bare. 2nd joint with ventral and medial spines and with lavender pigment. 3rd joint short, with 2 bristles (1 ventral, 1 dorsal). 4th joint with 2 bristles (1 ventral, 1 dorsal). Sensory bristle of 5th joint with 6 long proximal filaments and 3–4 short distal filaments. Medial bristle of 6th joint with faint marginal spines. 7th joint: a-bristle about same length as bristle of 6th joint but thicker, with faint marginal spines; b-bristle about twice length of a-bristle, with 3 marginal filaments; c-bristle long, with short marginal filaments (obscure on specimen examined). 8th joint: d- and e-bristles bare; f- and g-bristles long with short marginal filaments (bristles obscure on specimen examined).

SECOND ANTENNA (Fig. 9b). Protopodite similar to that of adult female. Exopodite: ventral margin of bristle of 2nd joint with 8 stout teeth followed by 4 smaller teeth; 9th joint with 1 short and 3 long bristles and pointed lateral spine; joints 5–8 with pointed basal spines; bristles of joints 3–8 and bristles of 9th joint with natatory hairs, no spines. Endopodite 3-jointed (Fig. 9b): 1st joint cylindrical with 1 long and 1 short proximal bristle and 1 long, more distal bristle; 2nd joint longer than 1st joint, bare; 3rd joint about $\frac{3}{4}$ length of 2nd joint; inner margin with 1 long proximal bristle with blunt tip (bristle twice length of 3rd joint), and stout, ringed, terminal bristle $\frac{1}{3}$ to $\frac{1}{2}$ length of 3rd joint.

MANDIBLE. Coxale basale, exopodite, and 1st endopodial joint similar to those of adult; 2nd endopodial joint with fewer short knife-like bristles on medial surface near dorsal margin, otherwise similar to that of adult; end joint similar to that of adult except longest lateral claw 45–47% length of 2nd endopodial joint.

MAXILLA. Endite I with 5 bristles; bristles of endites II and III obscure on specimen studied. 2nd endopodial joint with 3 b-bristles, and with fewer marginal spines on a-d-bristles; limb otherwise similar to that of adult male.

FIFTH LIMB. Exopodite: main tooth of 1st joint comprising small, bare, pointed peg and 4 constituent teeth (posterior tooth well developed with 6 marginal teeth; anterior tooth large with 6 or 7 marginal teeth at mid-length); bristle proximal to peg with few marginal spines; 2nd joint with 4 pectinate a-bristles (longest of these with 5–6 marginal teeth), 5b'- and b"-bristles (longest of these with 13 stout teeth and 3 small proximal

spines), 1 posterior c-bristle with long proximal hairs and short distal spines, and 1 hirsute anterior d-bristle; inner lobe of 3rd joint with 2 bristles (proximal short, with long proximal hairs and short distal spines; distal long, with short marginal spines); outer lobe of 3rd joint with short proximal and longer terminal bristle, both with short marginal spines; 4th and 5th joints fused, with 3 bristles, all with marginal spines; outer lobe of 3rd joint and fused 4th and 5th joints hirsute.

SIXTH LIMB. Limb with lavender pigment; 2 bristles in place of epipodial appendage; endite I with 2 bristles (1 long terminal, 1 short, medial); endite II with 2 short medial bristles and 1 long terminal bristle; endite III with 1 or 2 medial bristles and 2 terminal bristles (1 long, 1 short); endite IV with 4 bristles; end joint hirsute, with 13 bristles (posterior 2 bristles plumose, others with long proximal and short distal spines, or only short spines); with exception of 2 plumose posterior bristles, bristles of posterior third of end joint with bases medial and proximal to ventral margin of joint.

SEVENTH LIMB. Each limb with 2 proximal bristles (1 on each side) with 1 terminal bell and spear-like clapper emerging from center of bell, and 2 terminal bristles (1 on each side) also with 1 terminal bell and spear-like clapper; all bristles strongly tapering. Terminal comb

with spinous middle tooth only slightly longer than 4 lateral spinous teeth (2 teeth on each side of middle tooth); jaw opposite comb terminating in 3 prongs with marginal spines.

FURCA. Similar to that of adult.

EYES. Medial eye bare, with brown pigment in dorsal half, and appearing darker along midline. Lateral eye large, with black pigment and about 25 ommatidia (exact number uncertain because of obscurity caused by pigment).

BELLONCI ORGAN. Proximal part about twice diameter of finger-like distal part; tip blunt.

EYES, POSTERIOR OF BODY, Y-SCLERITE, UPPER LIP. Similar to those of adult.

COPULATORY LIMB. Not observed.

Description of A-2 female (instar IV) (Fig. 9c,d). Carapace similar to that of A-2 male (Fig. 9c).

SIZE. AM P36250, length 1.92 mm, height 1.37 mm.

SURFACE ORNAMENTATION. Similar to that of adult.

INFOLD. Rostral infold and infold of caudal process similar in structure to that of adult, but bristles not counted.

CENTRAL ADDUCTOR MUSCLE ATTACHMENTS, SELVAGE. Similar to that of adult.

PIGMENTATION. Similar to that of A-2 male.

FIRST ANTENNA. Similar to that of A-2 male.

SECOND ANTENNA. Protopodite similar to that of A-2 male. Exopodite: bristle of 2nd joint with 10 stout teeth followed by 5 smaller teeth, limb otherwise similar to that of A-2 male. Endopodite 3-jointed: 1st joint with 1 long and 1 short proximal bristle and 1 long, more distal bristle; 3rd joint about same length as 1st joint, bare; 3rd joint short, with long terminal bristle.

MANDIBLE. Similar to that of A-2 male; longest lateral claw of end joint 46–48% length of 2nd endopodial joint.

MAXILLA. Endites I and II each with 6 bristles. Only left limb without stout b-bristle, and with only 2 a-bristles. Limbs otherwise similar to those of A-2 male.

FIFTH LIMB. Similar to that of A-2 male except for slightly different number of marginal teeth on teeth of 1st and 2nd exopodial joints.

SIXTH LIMB. Endites similar to those of A-2 male; end joint similar to that of A-2 male except with 15 bristles; 1 bristle in place of epipodial appendage.

SEVENTH LIMB. Similar to that of A-2 male.

FURCA. Similar to that of adult.

BELLONCI ORGAN (Fig. 9d). Broad proximally and then tapering to pointed tip.

EYES (Fig. 9d). Similar to those of A-2 male.

POSTERIOR OF BODY, Y-SCLERITE, UPPER LIP. Similar to those of adult.

Description of A-1 male (instar V) (Fig. 9e,f). Carapace similar to that of A-2 male (Fig. 9e), but without lavender pigment.

SIZE. AM P36136, length 2.34 mm, height 1.80 mm.

FIRST ANTENNA. Joints 1–4 similar to those of A-2 male; sensory bristle of 5th joint with 8 long proximal filaments and 4 short distal filaments (distal of these minute); medial bristle of 6th joint similar to that of

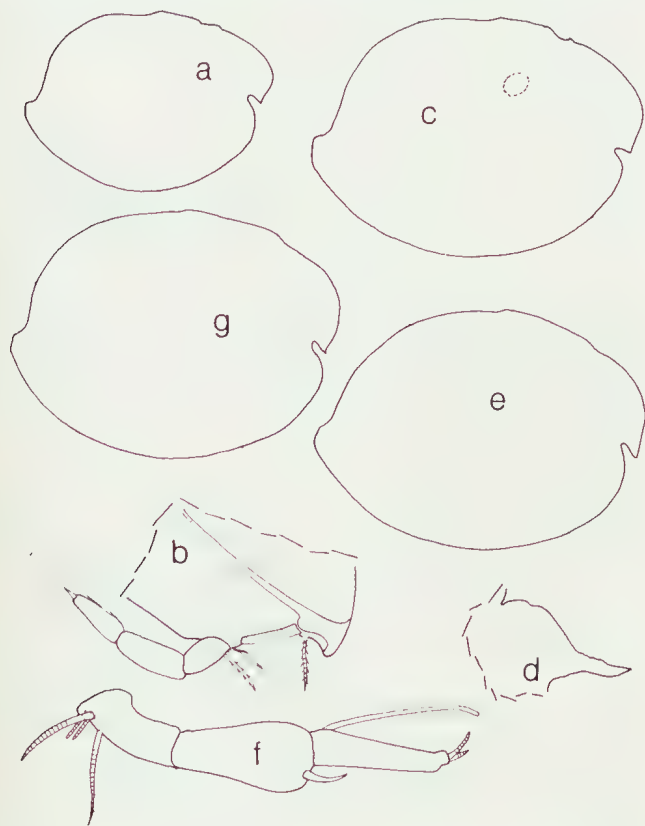


Fig. 9. *Codonocera cuspidata*, male instar IV paratype [AM P36140]: a, carapace from right, length 1.83 mm; b, distal part of protopodite, and endopodite of left 2nd antenna. Female instar IV paratype [AM P36250]: c, carapace from right (lateral eye dashed), length 1.92 mm; d, medial eye and Bellonci organ. Male instar V paratype [AM P36136]: e, carapace from right, length 2.34 mm; f, endopodite of right 2nd antenna. Female instar V paratype [AM P36138]: g, carapace from right, length 2.63 mm.

adult. 7th joint: a-bristle similar to that of adult; b-bristle similar to that of adult female, but with only 4 marginal filaments; c-bristle long, with many filaments (not counted). 8th joint: d- and e-bristles similar to those of adult; f- and g-bristles long with many filaments (not counted).

SECOND ANTENNA. Protopodite similar to that of adult female. Exopodite: ventral margin of bristle of 2nd joint with 11 rounded teeth followed by 5 pointed spine-like teeth; bristles of joints 3–9 similar to those of adult; basale spines small; lateral spine of 9th joint about same length as joint, with rounded tip and minute spine on each side near tip. Endopodite 3-jointed (Fig. 9f): 1st joint cylindrical, with 1 long and 2 short proximal bristles and 1 long more distal bristle; 2nd joint longer than 1st joint, widening distally, with 1 short bristle on outer margin and 3 weakly developed teeth lateral to base of bristle; 3rd joint thinner but slightly longer than 2nd joint, with 1 long proximal bristle on inner margin and 2 small ringed terminal bristles; 3rd joint not reflexed on 2nd as on adult male.

MANDIBLE. Coxale, basale, and 1st endopodial joint with pink pigment, and having similar number of bristles to adult, except for basale having only 2 a-bristles. Exopodite similar to that of adult. 2nd endopodial joint with fewer knife-like bristles than on adult. End joint with 6 bristles similar to those of adult; longest lateral claw 41–44% length of 2nd endopodial joint.

MAXILLA. 2nd endopodial joint: outer a-bristle with 4 spines along each edge; middle a-bristle with 5 spines along anterior edge and 4 along posterior edge; inner a-bristle with 8 spines along anterior edge and 1 along posterior edge; with 4 b-bristles. Limb otherwise similar to that of adult.

FIFTH LIMB. Exopodite: main tooth of 1st joint comprising small, bare, pointed peg and 5 constituent teeth (posterior tooth well developed with 4 marginal teeth; anterior tooth large with 2–3 small proximal teeth); bristle proximal to peg with few marginal spines; 2nd joint with 5 pectinate a-bristles (longest of these with 6 marginal teeth), 5 b'- and b''-bristles (longest of these with 14 marginal teeth), 1 posterior c-bristle with long proximal hairs and short distal spines, and 1 hirsute anterior d-bristle; inner lobe of 3rd joint with 2 bristles (proximal bristle short with long proximal hairs and short distal spines; distal bristle long with short marginal spines); outer lobe of 3rd joint with short proximal and longer terminal bristle, both with short marginal spines; 4th and 5th joints fused, with 3 bristles with short marginal spines; outer lobe of 3rd joint and fused 4th and 5th joints hirsute.

SIXTH LIMB. Limb with pink or lavender pigment. 3 bristles in place of epipodial appendage; endite I with 2–3 bristles (1 long terminal, 1–2 short medial); endite II with 2 short medial bristles and 2 terminal bristles (1 long, 1 short); endite III with 1 short medial bristle and 2 terminal bristles (1 long, 1 medium length); endite IV with 4 bristles; end joint hirsute, with 25 bristles (posterior 2 plumose, others with long proximal and

short distal spines, or only short spines); with exception of 2 plumose posterior bristles, bristles of posterior third of end joint with bases medial and proximal to ventral margin of joint.

SEVENTH LIMB. Each limb with 6 proximal bristles (3 + 3) with 1–3 bells, and 6 terminal bristles (3 + 3) with 1–4 bells; all bristles strongly tapering. Terminal comb with spinous middle tooth almost same length as adjacent spinous lateral teeth (3 on each side); jaw opposite comb curved, terminating in 3 prongs with marginal spines.

FURCA, EYES, BELLONCI ORGAN, POSTERIOR OF BODY, Y-SCLERITE, UPPER LIP. Similar to those of adult male.

Description of A-1 female (instar V) (Fig. 9g). Carapace similar in shape to that of A-2 female (Fig. 9g).

SIZE (length x height). AM P36138, 2.63 x 1.97 mm; AM P36139, 2.54 x 1.96 mm.

FIRST ANTENNA. Sensory bristle of 5th joint with 7 long terminal filaments and 4 short distal filaments (distal of these minute); limb otherwise similar to that of A-1 male.

SECOND ANTENNA. Protopodite similar to that of adult female. Exopodite: bristle of 2nd joint with 11 rounded teeth followed by 1 smaller pointed tooth; branch otherwise similar to that of A-1 male. Endopodite 3-jointed: 1st joint with 1 long and 2 short proximal bristles and 1 long, more distal bristle; branch otherwise similar to that of adult female.

MANDIBLE. Both limbs aberrant in having 3rd endopodial joint with 2 dorsal claws missing on right limb and 1 dorsal claw and 1 middle claw missing on left limb; longest lateral claw of end joint of right limb 45% length of 2nd endopodial joint; limb otherwise similar to that of A-1 male.

MAXILLA. 2nd endopodial joint: outer a-bristle with 5 spines along anterior edge and 4 along posterior edge; middle a-bristle with 7 spines along anterior edge and 3 spines along posterior edge; inner a-bristle with 10 spines along anterior edge and 2 spines along posterior edge; with 4 b-bristles, 2 c-bristles, and 3 d-bristles. Endite I with 5 bristles; endite II with 6 bristles; endite III with 6–7 distal bristles and 1 proximal bristle near base of endite. Limb otherwise similar to that of adult.

FIFTH LIMB. Similar to that of A-1 male; longest a-bristle of 2nd endopodial joint with 9 marginal teeth; longest of b'- and b''-bristles with 16 marginal teeth.

SIXTH LIMB. End joint with 20–23 bristles; limb otherwise similar to that of A-1 male.

SEVENTH LIMB. Similar to that of A-1 male.

FURCA, BELLONCI ORGAN, EYES, POSTERIOR OF BODY, Y-SCLERITE, UPPER LIP. Similar to those of adult female.

Ontogeny and sexual dimorphism (Table 1). In addition to adults, the collection contained a few A-2 instars and many A-1 instars. The A-2 instar is probably the 4th stage and the A-1 instar the 5th stage.

SHELL. The carapace of the juveniles have a dorsal margin more convex than that of the adult. The dorsal

margin of the adult male is less convex than that of the adult female. Juvenile males are larger than juvenile females, although the difference is less than for adults males and females (Table 1). Stellate lavender chromatophores, common in adults, were not observed in juveniles. Non-stellate lavender pigment was not observed in the A-2 instars, and only a slight amount was observed in the A-1 instars, whereas it is common in the adult. A pink colouration is present in both juveniles and adults, especially near the edges of the shells and around the periphery of calcareous nodules.

FIRST ANTENNA. A primary ontogenetic difference observed is an increase in the number of long proximal filaments on the sensory bristle of the adult. The abrupt increase from 8 to 20 during the development from A-1 to adult stages of the male suggests that filaments play a part in mating. The adult male bears clusters of suckers on the b- and c-bristles that are probably used for grasping the female during coupling.

SECOND ANTENNA. The number of small bristles on the 1st endopodial joints of both sexes increased from juveniles to adults (Table 1). The greatest development took place in the endopodite of the male. Its 2nd joint is cylindrical and bare in the A-2 instar, widens distally and bears 1 bristle in the A-1 instar, and further widens and bears 2 bristles as well as teeth on the adult; the 3rd joint bears 1 terminal bristle on the A-2 instar, and 2 on the A-1 instar and on the adult; the proximal part of the 3rd joint of the adult male is broad and crenulate, and the joint is reflexed on the 2nd. The endopodite of the adult male is thus capable of clasping the female while coupling.

MANDIBLE. Except for a smaller number of dorsal bristles on the 2nd endopodial joint, juvenile mandibles are similar to those of the adult.

MAXILLA. The number of b-bristles of the 2nd endopodial joint increased from 3 on the A-2 instar to 4 on the A-1 instar and to 5 on the adult.

FIFTH LIMB (Table 1). The number of constituent teeth of the main tooth of the 1st exopodial joint

increased from 4 on the A-2 instar to 5 on the A-1 instar and to 6 on the adult. A similar increase took place for the a-bristles of the 2nd exopodial joint. The b'- and b''-bristles increased from 5 on the A-2 and A-1 instars to 6 on the adult.

SIXTH LIMB. The bristles of the end joint increased at each stage (Table 1).

SEVENTH LIMB. The number of bristles increased from 4 to 12 in going from the A-2 to A-1 stage. Also, the bristles are very tapered in the A-2 stage, slightly tapered in the A-1 stage, and cylindrical in the adult.

FURCA, BELLONCI ORGAN, EYES, POSTERIOR OF BODY, Y-SCLERITE, UPPER LIP. Except for the A-2 male (AM P36140) having a Bellonci organ with a blunt tip, these characters are similar in juveniles and adults.

PIGMENTATION. Lavender pigment distributed in juveniles appendages as on adults. Pigment in appendages appearing as granules and not forming stellate patterns.

Remarks concerning shell nodules. Practically all specimens of *C. cuspidata* in the collection contain nodules in the shell. These nodules appear as flat discs generally oval in lateral view, or having linear edges where 2 or more discs are in contact. Discs are sparse in some shells and abundant in others. On some specimens the discs have a pink rim. Some of the specimens, primarily the juveniles, have small discs forming in a layer medial to larger discs; the smaller discs are entirely pink. Bate & Sheppard (1982: 29) contend that discs are formed as a step in shell calcification, and that shells become calcified by the coalescing of discs; whereas, Sohn & Kornicker (1969: 99) concluded that discs are formed mostly after death of the animal.

Station data recorded at time of collecting mentions that the specimens were bright lavender to pink. If nodules are formed after death of the animal, it follows that the concentration of pink pigment in, or around the periphery of, nodules probably also takes place after death.

Table 1. Selected characters changing during ontogeny.

Character	A-2		A-1		Adult	
	♀	♂	♀	♂	♀	♂
Shell length, mm	1.92	1.83	2.63	2.34	3.45	2.83
1st antenna, long filaments on sensory bristle	6	6	7	8	9-10	20
2nd antenna, bristles on 1st endopodial joint	3	3	4	4	4-5	5
Maxilla, b-bristles	3	3	4	4	5	5
5th limb						
Main tooth, constituent teeth	4	4	5	5	6	6
2nd joint, a-bristles	4	4	5	5	6	6
b' + b''-bristles	5	5	5	5	6	6
6th limb						
Bristles on end joint	15	13	20-23	25	26-28	32-34
Epipodial bristles	1	2	3	3	4	4-5
7th limb						
Proximal bristles	2	2	6	6	6	6
Terminal bristles	2	2	6	6	6	6
Bells on each bristle	1	1	1-4	1-4	3-7	3-7
Comb teeth	5	5	7	7	9	9

Table 2. Summary of characters by which the various species of *Codonocera* in the *cruenta* group may be distinguished.

	<i>cruenta</i>	<i>mortenseni</i>	<i>elongata</i>	<i>weberi</i>	<i>stellifera</i>	<i>cuspidata</i>
Length of mature specimens, ♂-♀, mm	3.2-3.9	-3.2	3.5-	-2.6	-3.9	2.8-3.5
Post. shell-process square (s) or rounded (r)	s	s	s	r	r	s
Grooves medially on shell margin below incisur	+	-	few	-	-	-
1st ant., 1st joint + or - ventral spine	-	-	-	-	+	-
1st ant., no. of filaments, ♂-♀, sensory bristle	50-15	-15	23-	-12	-12	24-14
Mandible end joint						
Length of longest claw in % of 2nd endop. joint	46	46	52	50	40	40-47
Longer dorsal claw + or - marginal spines	♂ +, ♀ -	-	-	-	-	-
Shorter dorsal claw + or - marginal spines	-	-	+	+	+	+
Longer ventral bristle + or - marginal hairs	-	-	+	-	-	+
Maxilla, longer posterior c - bristle + or - hairs or spines	+	+	-	+	+	+
Fifth limb						
Main tooth, no. of constituent teeth	6	6	6	5	6	6
Largest const. tooth + or - marginal teeth	-	+	-	-	+	+
2nd joint, no. of a-bristles	6	6	5	5	6	6
Smallest a-bristle + or - marginal teeth	+	-	+	+	+	+
Largest a-bristle + or - marginal teeth	+	+	+	+	+	+
No. b' - + b''-bristles	5	5	6	6	6	6
No. of teeth on longer b' - + b''-bristles	12-14	10-14	17-20	15-19	14-17	14-16
3rd joint, outer lobe, longer bristle + or - hairs	+	+	+	-	-	+

Comparisons. Bate & Sheppard (1982: 26) reported *Codonocera polygonia* Müller, 1906, from Wisteri Channel, Heron Island, on the Great Barrier Reef, Australia. The new species *C. cuspidata* differs from *C. polygonia* in having a total of 6 rather than 5 claws and bristles on the end joint of the mandible, and 6 rather than 5 constituent teeth on the 1st exopodial joint of the 5th limb, as well as in numerous other characters (for detailed description of *C. polygonia* see Poulsen, 1962: 311, 35). Characters in which *C. cuspidata* differ from other members of the *cruenta* group are shown in Table 2, which is adapted from Poulsen (1962: Table 21). Although not listed in the table, the armature of the tip of the 7th limb is also useful in discriminating species of the *cruenta* group. The middle comb tooth is only slightly longer than the adjacent lateral teeth in *C. cuspidata*, whereas it is twice the length in *C. mortenseni* Poulsen, 1962, *C. stellifera* (Claus, 1873), and possibly *C. weberi* Poulsen, 1962. The jaw opposite the comb of the 7th limb forms a curving tusk in *C. cuspidata*, whereas it is fairly linear in *C. cruenta*. The jaw opposite the comb of *C. cuspidata* bears marginal spines not observed by Poulsen (1962: 322, 327) on *C. mortenseni* and *C. elongata* Poulsen, 1962. The new species *C. cuspidata* seems closest in morphology to *C. elongata* from which it differs in having a pectinate rather than a bare posterior c-bristle on the maxilla, and in having 6 rather than 5 a-bristles on the 5th limb, as well as the difference in the jaw of the 7th limb mentioned above. *Codonocera elongata* and *C. cuspidata* both have pointed tips on the Bellonci organ, and not blunt tips as on the other species in the *cruenta* group, according to Poulsen (1962: 310). *Codonocera formosa* (Dana, 1852) is insufficiently known for recognition; therefore, I refer it to *Codonocera* species indeterminate". Two species, *C. pusilla* Müller, 1906 and *C. penicillum* Müller, 1906, insufficiently known to place either in the *cruenta* or *goniacantha* groups, differ from *C. cuspidata* in having a ventral spine on the 1st joint of the 1st antenna. *Codonocera cuspidata* bears a basal bristle on the coxale endite of the mandible not previously reported on species of *Codonocera*.

ACKNOWLEDGEMENTS. My thanks to James K. Lowry, The Australian Museum, for permitting me to study the specimens described herein; to P. S. Davis, The Hancock Museum, for loan of the holotype of *C. cruenta*; to Carolyn Gast, Smithsonian Institution, for the shaded rendering of the carapaces; and to Thomas E. Bowman, Smithsonian Institution, for commenting on the manuscript.

References

- Barney, R.W., 1921. Crustacea, V: Ostracoda. In British Antarctica ("Terra Nova") Expedition, 1910 Natural History Report, Zoology 3(7): 175-190.
- Bate, Raymond H., & Lesley M. Sheppard, 1982. The shell structure of *Halocypris inflata* (Dana, 1849). In "Fossil and Recent Ostracods" (R. H. Bate, E. Robinson & L. M. Sheppard, editors): 25-50. Ellis Horwood Limited, Chichester, for the British Micropalaeontological Society.
- Brady, G.S., 1902. On new or imperfectly-known Ostracoda, chiefly from a collection in the Zoological Museum, Copenhagen. Transactions of the Zoological Society of London SVI (4): 179-211, 25 pls.
- Claus, C., 1873. Neue Beobachtungen über Cypridinen. Zeitschrift für Wissenschaftliche Zoologie 23(2): 211-227, 31 figs.
- McKenzie, K.G., 1967. The distribution of Caenozoic marine Ostracoda from the Gulf of Mexico to Australasia. In "Aspects of Tethyan Biogeography" (C. G. Adams & D. V. Ager, editors). Systematics Association Publication 7: 219-238.
- Müller, G. W., 1906. Die Ostracoden der Siboga-Expedition. In Uitkomsten op Zoologisch, Botanisch, Oceanographischen en Geologische gebied versameld in Nederlandsch Oost-Indie, 1899-1900, 30: 40 pp, 9 pls. Leiden, E. J. Brill.
- Poulsen, E. M., 1962. Ostracoda-Myodocopa, 1: Cypridiniformes-Cypridinidae. In Dana Report 57: 1-414, 181 figs. Carlsberg Foundation, Copenhagen.
- Skogsberg, T., 1920. Studies on Marine Ostracodes, 1: Cypridinids, Halocyprids, and Polycopids. Zoologiska Bidrag från Uppsala (supplement), 1784 pp, 153 figures.
- Sohn, I. G., & Louis S. Kornicker, 1969. Significance of calcareous nodules in myodocopid ostracod carapaces. In "The taxonomy, morphology and ecology of Recent Ostracoda" (J. W. Neale, editor): 99-108. Oliver and Boyd, Edinburgh.

Thrypticus and an Allied New Genus, *Corindia*, from Australia (Diptera: Dolichopodidae)

DANIEL J. BICKEL

Australian Museum,
P.O. Box A285, Sydney South, NSW 2000, Australia

ABSTRACT. *Corindia* n. gen. and Australian *Thrypticus* Gerstäcker are described, including nine and three new species, respectively: *C. major*, *C. minor*, *C. capricornis*, *C. collessi*, *C. nigricornis*, *C. robensis*, *C. cooloola*, *C. torresiana* and *C. trudis*; *T. australis*, *T. tropicus* and *T. fortescuensis*. The two genera have a sister-group relationship and their phylogenetic position within the subfamily Medeterinae is discussed. A lectotype is designated for *T. abditus* Becker. The New Zealand *Thrypticus nigrichaetus* Parent is regarded as *Chrysotimus nigrichaetus* (Parent), new combination.

BICKEL, DANIEL J., 1986. *Thrypticus* and an allied new genus, *Corindia*, from Australia (Diptera: Dolichopodidae). Records of the Australian Museum 38(3): 135-151.

While field collecting and sorting specimens in preparation for a monograph on the Indo-Australian *Medetera* Fischer von Waldheim, I have isolated a group of species which represent a new genus, *Corindia*, in the dolichopodid subfamily Medeterinae. All nine included new species are from Australia. Because of its close phylogenetic relationship with the cosmopolitan genus *Thrypticus*, I have also included a revision of the Australian members of this genus.

The Medeterinae is superficially distinguished from all other dolichopodid subfamilies by the following combination of characters: posterior mesoscutum distinctly flattened; femora II and III lacking anterior preapical bristles; hypopygium large, on elongate peduncle formed by abdominal segment 7; antennal scape without dorsal setae; arista apical; dorsal postcranium strongly concave; vein M unbranched and lacking a flexion (or *bosse alaire* of Parent) in the distal sector; frontoclypeal suture distinct, usually marked by a band of pruinosity; hypopygium with distal surstyli, divided into dorsal and ventral lobes; epandrial seta present ventrobasally; pair of epandrial lobes arising distally along ventral margin near base of surstylus, and each lobe bearing strong bristle (for further information on the Medeterinae, see Negrobov, 1971-77, and Bickel, 1985). The three included Australian genera, *Medetera*, *Corindia* and *Thrypticus*, are distinguished in the text key.

Materials and Methods

All measurements are in millimetres except for the podomere ratios which represent the relative lengths of the leg segments as given in the following formula: femur; tibia; tarsomere 1/2/3/4/5. The CuAx ratio is the quotient of lengths: m-cu crossvein/distal segment of CuA, from crossvein to wing margin. The morphological terminology follows McAlpine (1981) and Bickel (1985). In describing the hypopygium, 'dorsal' and 'ventral' refer to morphological position prior to genitalic rotation and flexion. Thus, in figures showing a lateral view of the hypopygium, the top of the page is morphologically ventral, while the page bottom is dorsal. The position of features on elongate structures is given as a fraction of the total length, starting from the base.

The following abbreviations were used:

- AMS Australian Museum, Sydney
- ANIC Australian National Insect Collection, Canberra
- NVM Museum of Victoria, Melbourne
- NZAC New Zealand Arthropod Collection, Auckland
- SAM South Australian Museum, Adelaide
- USNM United States National Museum, Washington, D.C.
- ZMUA Zoologisch Museum, Amsterdam

Key to Genera of Australian Medeterinae and Species of *Corindia* and *Thrypticus*

1. Wing vein M distinctly curving towards $R_4 +_5$ beyond m-cu crossvein; coxa III with only 1 lateral seta; eyes bare; 2 supraalars (sa) present, the posterior stronger and anterior weaker; femur II without posterior subapical seta; anal vein usually distinct; body coloration usually black or dark metallic green; hypandrium arising mid-ventrally from epandrium. *Medetera*
- $R_4 +_5$ and M parallel to apex; coxa III with 2 lateral setae; eyes with short hairs between facets; only 1 supraalar (sa) present; femur II with strong posterior subapical seta; anal vein indistinct or absent; body coloration usually bright metallic green; hypandrium arising basoventrally from epandrium. 2
2. Female oviscapt broad, cylindrical, with 2 pairs of dorsal spines (Figs 4, 5); epandrial lobes separate, each bristle arising from a short basal collar; surstylus not strongly deflexed dorsad; cerci not conforming to dorsal surstylar margin; cerci with long distolateral arms, much longer than the broad cercal base from which they arise; anal vein present as weak fold; CuAx ratio > 0.5 , i.e., m-cu relatively close to posterior margin of wing; aedeagus usually with deep apicoventral notch. *Corindia* ... 3
- Female oviscapt blade-like, sclerotized, narrow in dorsal view (Figs 23, 24); epandrial lobes fused into elongate collar from which the 2 bristles arise; surstylus strongly deflexed dorsad, usually lying conformably with similarly deflexed, oblong-shaped cerci; cerci without distolateral arms; CuAx ratio usually < 0.5 , i.e., m-cu somewhat distant from posterior margin of wing; aedeagus usually bifurcate apically. *Thrypticus* ... 11
3. Antenna entirely dark brown. 4
- Antennal scape and pedicel yellow or red-yellow. 6
4. Male femur III with a mid-ventral cuticular projection bearing a tapering seta (Fig. 13); legs dark brown; thoracic setae black; ventral arm of surstylus with stout conical seta, subtended along ventral margin by a strong curved seta; a striated blade-like seta arising on a pedicel between the dorsal and ventral surstylar arms (Fig. 12). *C. trudis*
- Male femur III unmodified; at least tibiae yellowish; thoracic setae yellow-brown. 5
5. Hypandrium with paired ventral thorn-like projections at $\frac{5}{6}$; surstylus with distinctive dorsoapical clavate projection, and with long hooked seta; cercus with elongate bare distolateral arm (Fig. 15). *C. robensis*
- Hypandrium without flexion or ventral projections; surstylus with distinctive dorsal subapical cuticular hook; cercus with short distolateral arm (Fig. 14). *C. nigricornis*
6. Aedeagus with strong dorsal triangular projection; surstyli with short curved seta on ventral margin; hypandrium with only slight bumps near hypandrial flexion (Fig. 7). *C. collessi*
- Aedeagus clavate, apically expanded (e.g. Fig. 1); surstyli without a short stout curved seta on ventral margin; hypandrium with a pair of ventral thorn-like projections near flexion. 7
7. Distolateral cercal arm stout, with long curved apical setae as long as arm itself (Figs 1, 2); surstyli wide in lateral view, arising from an elongate epandrium; female abdominal terga 1, 2 yellowish; length > 2.3 *C. major*
- Distolateral cercal arm peg-like, with straight apical setae, not longer than $\frac{2}{3}$ length of arm; surstyli relatively narrow in lateral view, arising out of bulbous epandrium; female abdomen unicolorous metallic green; length < 2.1 8

8. Hypandrium apically clavate, with ventral thorn-like projections and flexion at $\frac{2}{3}$; surstylus with distinctive curved dorsal arm (Fig. 9). *C. minor*
 —Hypandrium slightly tapering or subparallel apically, with ventral thorn-like projections at $\frac{5}{6}$; ventral surstylar arm arising medially, partially hidden in lateral view by longer dorsal arm. 9
9. Coxa I, femora dark brown; dorsal surstylar arm blunt, apex curved medially (Fig. 11); strong dorsal setae along distolateral arm of cercus; epandrial lobes arise internally such that lobe bases hidden in lateral view. *C. torresiana*
 —Coxa I, femora yellowish; dorsal surstylar arm tapering, fingerlike, not curved medially; at least middle section of distolateral arm of cercus bare, without dorsal setae. 10
10. Dorsal surstylar arm short and curved; distolateral cercal arm with strong seta at $\frac{3}{4}$ (Fig. 10). *C. capricornis*
 —Dorsal surstylar arm elongate, straight; distolateral cercal arm with only strong apical setae (Fig. 16). *C. cooloola*
11. Hypandrium beyond flexion triangular, broad basally, tapering distally, and heavily melanized (Fig. 18); surstylus with 2 distal short setae and strong ventral seta at $\frac{2}{3}$ (Fig. 17). *T. australis*
 —Hypandrium beyond flexion parallel-sided, narrow, with only slight basal melanization (Fig. 20). 12
12. Surstylus relatively long, as long as epandrium; apex of aedeagus not reaching distal margin of surstylus; surstylus rounded distally; strong seta present at $\frac{2}{3}$ along ventral margin of surstylus; body colour distinctly metallic blue-green (Fig. 22). *T. fortescuensis*
 —Surstylus shorter, distinctly shorter than epandrium; apex of aedeagus reaching distal margin of surstylus; surstylus projecting dorsally somewhat; strong seta present subapically on ventral margin of surstylus; body colour bright metallic green (Fig. 19). *T. tropicus*

Genus *Corindia* n. gen.

Type species. *Corindia major* n. sp.

Diagnosis. Body colouration usually bright metallic green; eyes with short hairs between facets; only 1 sa present; coxa III with 2 lateral setae; femur II with strong posterior subapical seta; wing veins $R_4 + s$ and M parallel to apex; CuAx ratio > 0.5 , i.e., m-cu relatively close to posterior margin of wing; anal vein present as weak fold; hypandrium arising basoventrally from epandrium, and usually with a flexion or indentation in distal third; hypopygial foramen in left basolateral position; aedeagus usually with deep apicoventral notch; epandrial seta strong, curved, internal, not visible in lateral view; epandrial lobes separate, each bristle arising from a short basal collar; surstylus not strongly deflexed dorsad; ventral margin of cercus not conforming to dorsal surstylar margin; cerci with long distolateral arms, much longer than the broad cercal base from which they arise; female oviscapt broad, cylindrical, with 2 pairs of dorsal spines.

Description. The following description of *Corindia* is based on the nine included new species.

HEAD: postcranium strongly concave dorsally; vertex

slightly excavated, ocelli on small tubercle; single pairs of vertical, ocellar and short postvertical setae present; frons, face slightly wider in females than in males, usually bright metallic green-blue, of coriaceous texture, and sometimes with faint longitudinal furrows; frontoclypeal suture complete, marked above by transverse band of pruinosity; clypeus metallic green-blue; antennal pedicel and scape short, usually yellowish; 1st flagellomere subrectangular, dark brown; arista apical, bare, about $1\frac{1}{2}$ head height in length; eyes with short setulae between facets; palpi black with strong apical seta; proboscis dark brown, relatively small, not massive and heavily sclerotized as in many *Medetera*; labrum not elongated; epipharyngeal armature with 2 prongs; labella with 6 pseudotracheae, ribbon-like, unsclerotized (mouthpart structure similar to Group IV of Cregan, 1941); single row of pale postorbitals, ventralmost strong, projecting over posterior portion of proboscis; ventral postcranium with few scattered pale setae.

THORAX: posterior portion of mesonotum distinctly flattened, even slightly concave; colour metallic blue or green, with thin pruinose covering; 10–12 pairs acrostichals (ac) present, ending before mesonotal

depression, about as long as width of ac band; 5 strong dorsocentrals (dc) present, decreasing in size anteriorly, anteriormost just in front of mesonotal suture, with anterior short setulae which extend laterally as a field towards postpronotum (humeral callus); 1 postalar (pa) present; only 1 postsutural supraalar (sa) present, corresponding to posterior sa of the 2 sa in *Medetera*; 1 presutural intraalar (sr), 1 strong presutural supraalar (pm), 2 short postpronotals (hm) present; 2 notopleurals (npl) present, almost adjacent, positioned much closer together than in *Medetera*; 1–3 proepisternals (ppls); paired median and lateral marginal scutellar bristles present, laterals reduced to weak hairs, usually less than $\frac{1}{3}$ length medians.

LEGS: coxae I and II with short anterior setulae; coxa III with 2 lateral bristles, dorsal longer than ventral; femur II with strong posterior subapical seta; tibia II with anterodorsal seta at $\frac{1}{4}$ (posterodorsal absent), and with strong ventral apicals; all legs with paired apical claws.

WINGS: hyaline; $R_4 + 5$ and M parallel to wing margin (Fig. 6); anal vein as weak fold almost to margin; anal cell indistinct; CuAx ratio greater than 0.5, i.e., m-cu crossvein relatively close to posterior wing margin.

ABDOMEN: cylindrical with short setulae; terga 2–5 with 2–3 ovoid depressions along lateral margins; male sterna modified to receive hypopygium, which at rest is tucked up and slightly enfolded by the abdomen so that surstylar tips are held near coxa III; male sterna 6 and 7 reduced to narrow bands, sterna 3–5 mid-ventrally weakly sclerotized and concave, with marginal excavations posteriorly; female sterna normal, forming collar-like bands without posterior excavations; spiracles present in membrane between terga and sterna 1–6.

MALE POSTABDOMEN: tergum and sternum 7 fused and somewhat rotated to left lateral position, forming trapezoidal hypopygial peduncle pivoting on tergum 6; sternum 8 forming cap over hypopygial foramen, tergum 8 absent; hypopygium with epandrium (= tergum 9) forming elongate, somewhat cylindrical capsule with left basal hypopygial foramen (see Fig. 1); single strong curved epandrial seta positioned ventrobasally arising from lateral internal epandrial wall and not visible externally in lateral view; 2 epandrial lobes arising from apodeme near ventral margin of epandrium, adjacent, each with collar-like base bearing strong projecting bristle; hypandrium not fused to epandrium, but with membranous attachment, allowing it to be raised and lowered against epandrium; hypandrium arising far basad along ventral margin of epandrium, forming elongate cover over aedeagus, usually with flexion and accompanying ventral protuberance (usually paired and thorn-like) within distal $\frac{1}{3}$, and sometimes with serrated or hair-like fringe at tip of hypandrium (Fig. 3); aedeagus elongate, arising from internal ejaculatory bulb near hypopygial foramen, curving basad to emerge under base of hypandrium, and extending almost to tips of surstyli, often with distinctive deep subapical notch on ventral margin; surstyli fused to epandrium without noticeable

suture line, usually with dorsal and ventral arms bearing species-specific setae and projections; cercus with basal pilose section from which projects distolateral arm bearing long setae (Fig. 2).

FEMALE TERMINALIA (Figs 4,5): abdomen telescoped, with 5 visible segments concealing 4, often retracted segments of oviscapit; segments 6, 7, 8 smooth and polished, with fused terga and sterna, projecting collar-like from segment 5; 2 elongate internal rods adjoin fused segment 9+10; segment 9+10 with 2 pairs of dorsal peg-like projections or spines (possibly homologous to the acanthophorites of lower Brachycera); pair of cerci arise ventrolaterally from segment 9+10.

Bionomics. Adult *Corindia* are often found on the trunks of smooth-barked *Eucalyptus* and *Angophora* trees. Here they display a stance similar to that of *Medetera*, a vertical upright posture, with the body leaning outwards, such that the abdomen makes an angle with the surface. When disturbed, they run rapidly sideways or backwards, or fly a short distance to land laterally and somewhat higher about $\frac{1}{4}$ to $\frac{1}{3}$ around the trunk's circumference, always maintaining the upright posture. I have observed individuals of *C. major* using these short flights to irregularly spiral up the boles of huge, smooth-barked eucalypts until out of sight. Some specimens were seen flying down parallel to the trunk to land near the base and thereby initiate another ascent.

Congregations of *Corindia* on tree trunks presumably function as leks to facilitate mating, as is the case with *Medetera* (Bickel, 1985). Males of *C. major* have been observed to approach females (and sometimes other males) from behind and attempt to copulate by thrusting their abdomens forward between their legs towards the terminalia of their prospective mates. Coupling has been observed in *Corindia* (either *C. major* or *C. cooloola*), the mated pair resting upright on the trunk of *Eucalyptus* sp., and with the male posterior to and partially covering the female. *Corindia* males lack prominent secondary sexual characters (except possibly the ventral cuticular projection on femur III of *C. trudis*), and mating display, common among more ornamented male dolichopodids, has not been observed.

Nothing is known of the immature stages of *Corindia*. However, I have observed a gravid female *C. minor* apparently ovipositing in bark fissures on a healthy black wattle, *Acacia* near *decurrens*. This suggests a possible subcortical habitat for the larvae, similar to that of many *Medetera*.

Corindia is apparently endemic to Australia, with a distribution along the southern and eastern coasts and ranges from South Australia and Tasmania, to Queensland, and across tropical northern Australia. Considering the far northern distribution of some *Corindia* species, including the Torres Strait Islands, the genus may extend into the Papuan region. However, I have not seen the genus in any collection of New Guinea dolichopodids, including the extensive Bishop Museum holdings.

Etymology. *Corindia* is derived from Corindi, a geographical place name of aboriginal origin on the New South Wales northern coast, and the gender is feminine.

***Corindia major* n. sp.**

Type material. HOLOTYPE ♂; PARATYPES 10 ♂♂, 9 ♀♀: New South Wales: Corindi Creek, Red Rock, 15 km N of Woolgoolga, 7-xi-1980, on trunks *Eucalyptus propinqua*, coastal forest, leg. D.J. Bickel (Holotype, 4 paratypes, AMS; 15 paratypes, ANIC).

Additional material examined. New South Wales: Tahmoor,

18-ii-1981 (AMS); Mosman, Ashton Park, 12-ii-1984, 26-xii-1984, on trunks *Angophora costata* (AMS); Myall Lakes National Park, on *A. costata*, 21-xi-1985 (AMS); Putty Rd at Tinda Creek, 20 km N of Colo Heights, 17-ii-1984, on trunks *Eucalyptus haemastoma* (AMS); nr. Buladelah, 11-xii-1985, on *E. grandis* (AMS). **Queensland:** Coolool National Park, on *Eucalyptus* sp., 27-xi-1985 (AMS). **Tasmania:** Melaleuca Inlet, SW Coast, 3-ii-1966 (MVM).

Unassociated females possibly representing this species: **Queensland:** 1 km N of Rounded Hill, 15°17'S 145°13'E, 5-x-1980, at light (ANIC); 3 km E of Mt Webb, 15°03'S 145°09'E, 1-x-1980, at light (ANIC); **Western Australia:** Millstream, 21-x-1970, at light (ANIC), (18 ♂♂, 26 ♀♀ specimens examined)

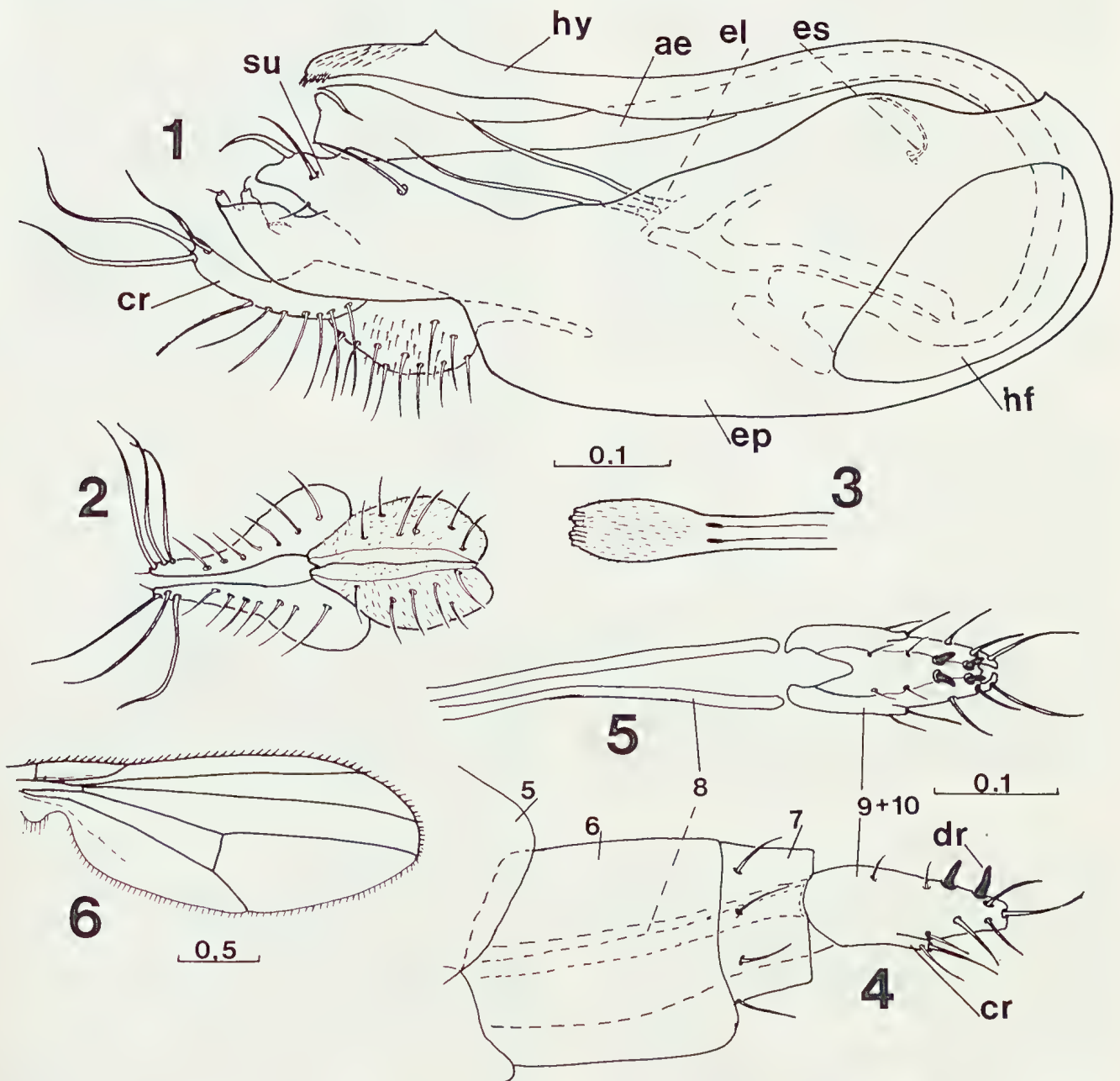


Plate 1

Figs 1-6. *Corindia major*, Red Rock, NSW. 1, Hypopygium, left lateral view: ae, aedeagus; cr, cercus; ep, epandrium; el, epandrial lobe; es, epandrial seta; hf, hypopygial foramen; hy, hypandrium; su, surstylus. 2, Cerci, dorsal view. 3, Apex of hypandrium, ventral view. 4, Female terminalia, dorsal view: cr, cercus; dr, dornen; 5, 6, 7, 8, 9+10, abdominal segments. 6, Right wing, dorsal view.

Description. MALE: length 2.4–2.7.

HEAD: vertex, frons, metallic blue-green, covered with grey pruinosity; face satiny metallic blue-violet, with green reflections; clypeus metallic blue-green; palpi and proboscis dark brown; scape and pedicel orange-yellow, 1st flagellomere brown.

THORAX: metallic blue-green with dusting of grey pruinosity dorsally and laterally; margin of scutellum yellowish; setae brownish; 2–3 pale ppls; lateral scutellars $\frac{1}{3}$ length of medians.

LEGS: coxa I pale yellow to infuscated brownish green in older specimens; coxae II and III brownish; legs otherwise yellow although femora sometimes infuscated; podomere ratios as I: 2.4; 1.8; 0.9/0.6/0.4/0.3/0.2. II: 2.4; 2.2; 1.2/0.7/0.5/0.3/0.2. III: 2.3; 2.8; 0.7/1.3/0.7/0.3/0.2.

WINGS: dimensions 1.9 x 0.8 (Fig. 6); CuAx ratio 0.7–0.9; lower calypter, halter pale yellow.

ABDOMEN: male abdomen entirely metallic bronze-green with pale setulae, covered with dusting of grey pruinosity; hypopygium (Fig. 1), epandrium elongate (compare with more spherical shape in other *Corindia*); hypandrium with paired ventral thorn-like projections at $\frac{5}{6}$, and with apical fringe of 8 hair-like cuticular projections (Fig. 3); aedeagus expanded apically with deep ventroapical notch; surstyli broad in lateral view with dorsal and ventral lobate arms, bearing setae as figured; cerci with stout distolateral arms which bear distinctive long curved setae (Fig. 2).

FEMALE: similar to male except as noted.

ABDOMEN: terga 1, 2 and 3 almost entirely yellow except for some dorsal infuscation; some specimens with tergum 1 entirely metallic green, and in apparently older specimens, tergum 2 and part of tergum 3 may exhibit some green coloration dorsally and laterally; sterna 2–5 yellowish; in many specimens, tip of oviscapt is upcurved (Figs 4, 5).

Remarks. *Corindia major* is found along the eastern coast of Australia from southern Queensland to Tasmania, and is a relatively common species, especially in dry sclerophyll forests. Isolated female specimens from tropical Queensland and Western Australia which display yellowish abdominal terga and are in the approximate size range may represent this species.

Corindia collessi n. sp.

Type material. HOLOTYPE ♂; PARATYPES 4♂♂, 3♀♀: **Queensland:** Mt Cook National Park, 15°29'S 145°16'E, 10-v-1981, malaise trap, *leg.* D.H. Colless; PARATYPES 5♂♂: same data except 12-v-1981, taken at light; PARATYPES 3♂♂: **Western Australia:** Carson Escarpment, 14°49'S 126°49'E, 9 to 15-viii-1975, *leg.* I.F.B. Common & M.S. Upton (all ANIC).

Additional material examined. Two unassociated females possibly representing this species: **Northern Territory:** Caranbirini Waterhole, 33 km SW of Borroloola, 22-iv-1976, malaise trap. **Western Australia:** Millstream, 25-x-1970 (ANIC).

Description. MALE: length 2.2–2.4.

HEAD: vertex, frons metallic green with grey pruinosity; face metallic blue-green with faint longitudinal furrows and some grey pruinosity; clypeus metallic blue-green; palpi and proscis dark brown; scape and pedicel reddish yellow, 1st flagellomere brown, subrectangular.

THORAX: metallic green with bronze reflections, with grey pruinosity; setae pale to brownish; 1 pale ppl; lateral scutellars about $\frac{1}{4}$ length of medians.

LEGS: coxae dark brown, becoming paler distally; femora black; femoral 'knees', tibiae and basal tarsomeres yellowish; distal tarsomeres black; podomere ratios as I: 2.8; 2.3; 1.1/0.7/0.4/0.3/0.3. II: 3.0; 2.7; 1.4/0.9/0.6/0.4/0.3. III: 2.9; 3.2; 0.7/1.3/0.8/0.4/0.3.

WINGS: dimensions 1.9 x 0.8; CuAx ratio: 0.7; lower calypter and halter pale yellow.

ABDOMEN: metallic bronze-green, with grey pruinosity and short pale setulae; hypopygium (Fig. 7) small in relation to preabdomen, especially as compared with *C. major*; epandrial lobes arising near ventral margin of epandrium; hypandrium broad (Fig. 8), with flexion and slight ventral projections at $\frac{5}{6}$, apex slightly deflexed; aedeagus with strong dorsal triangular prominence, and with apical notch; ventral surstylar arm arising medially and partially covered by longer dorsal arm; dorsal surstylar arm narrowed and curved apically, with distinctive stout curved seta on ventral margin; other surstylar setae as figured; distolateral arm of cercus with 4–5 strong dorsal setae and with apical setae as figured.

FEMALE: similar to male; abdomen unicolorous metallic green.

Remarks. *Corindia collessi* is distributed across northern tropical Australia.

Corindia minor n.sp.

Type material. HOLOTYPE ♂; PARATYPES 6♂♂, 2♀♀: **New South Wales:** Mosman, Ashton Park, 12-ii-1984, on trunks *Angophora costata*, *leg.* D.J. Bickel (ANIC).

Additional material examined. **New South Wales:** Mosman, Ashton Park, on *A. costata*, 2-xii-1984 to 6-i-1985; Ku-ring-gai Chase National Park, on *A. costata*, 28-xii-1984; Port Hacking River, Royal National Park, subtropical rainforest, on trunks *Acacia* near *decurrens* and *Alphitonia excelsa*, 12-ii-1985. (15♂♂, 18♀♀, AMS).

Description. MALE: length 1.7–2.0. Similar to *C. collessi* except as noted.

HEAD: face shining metallic blue-green.

THORAX: metallic blue-green; lateral scutellars as weak hairs.

LEGS: coxae brown, becoming yellowish distally; legs otherwise yellow; podomere ratios similar.

WINGS: dimensions 1.8 x 0.8; CuAx ratio: 0.7.

HYPOPYGIUM (Fig. 9): hypandrium pinched with ventral thorns at $\frac{3}{4}$, and expanded, clavate apically; aedeagus strongly curved with deep ventroapical cleft; surstylus with distinctive curved dorsal arm, setae as figured; cercus with long projecting distolateral arm.

FEMALE: similar to male; abdominal terga 1–5

unicolorous metallic green.

Remarks. *Corindia minor* is commonly during the summer months in the Sydney district, and is found on the trunks of smooth-barked trees in habitats ranging from dry sclerophyll woodland to subtropical rainforest.

Corindia capricornis n. sp.

Type material. HOLOTYPE ♂; PARATYPES 3♂♂: **Queensland:** 1 km W of Cooktown, 15°28'S 145°15'E, 13-v-1981, malaise trap, leg. D.H. Colless; PARATYPES 2♂♂: same data except 10-v, 12-v. **Western Australia:** PARATYPE ♂: 8 km S of Cape Bertholet, 21-iv-1977; PARATYPE ♂: Crossing Pool, Millstream, 21-x-1970, at light (all ANIC).

Additional material examined. Two unassociated females probably representing this species: **Queensland:** Gap Creek, 5 km ESE of Mt Finnigan, 15°50'S 145°20'E, 13-v-1981; 3.5 km SW by S of Mt Baird, 15°10'S 145°20'E, 4-v-1981 (ANIC).

Description. MALE: length 1.6–1.7. Similar to *C. collessi* except as noted.

HEAD: vertex, frons metallic green with brown pruinosity; face metallic blue-green with faint longitudinal furrows.

THORAX: setae yellowish; strong median scutellars, laterals as tiny hairs.

LEGS: coxa I yellow, coxae II, III infuscated basally, yellowish distally; legs otherwise yellow, tarsi darkened

apically; podomere ratios similar.

WINGS: dimensions 1.4 x 0.8; CuAx ratio: 1.1; lower calypters and halteres yellow.

ABDOMEN: hypopygium (Fig. 10); epandrial lobes arise near ventral margin of epandrium; hypandrium with paired ventral thorn-like projections at $\frac{5}{6}$, and apical coarse serrations; aedeagus expanded distally, with deep apicoventral notch; ventral surstylar arm with setae as figured; dorsal surstylar arm tapering, fingerlike; distolateral cercal arm with 2–3 strong dorsobasal setae, bare mid-section, 1–2 strong dorsal subapical setae, and strong apical seta.

FEMALE: similar to male; abdomen unicolorous.

Remarks. *Corindia capricornis* is distributed across northern tropical Australia, and is broadly sympatric with *C. collessi*.

Corindia torresiana n. sp.

Type material. HOLOTYPE ♂: **Queensland:** Torres Strait, Banks Island, 3-vi-1969, sweeping grassy savannah, leg. A. Neboiss (MVM T-8076).

Description. MALE: length 2.0; similar to *C. collessi* except as noted.

THORAX: metallic blue-green with grey pruinosity; lateral scutellars as weak hairs, less than $\frac{1}{4}$ length of medians.

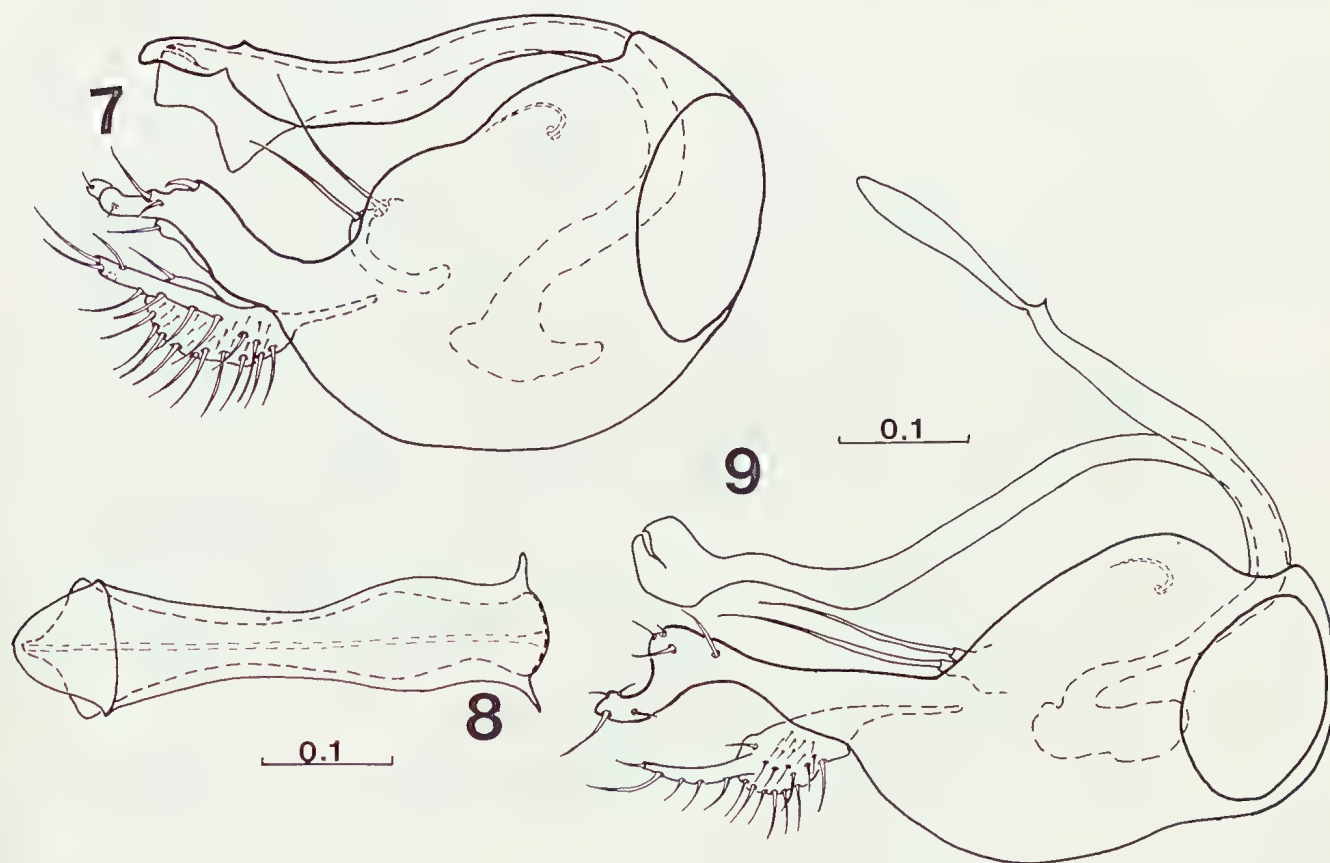


Plate II

Figs 7–8. *Corindia collessi*, Mt Cook, Qld. 7, Hypopygium, left lateral view. 8, Hypandrium and aedeagus, ventral view.
Fig. 9. *Corindia minor*, Mosman, NSW. Hypopygium, left lateral view.

LEGS: coxae dark brown, femora brown, legs otherwise yellowish; podomere ratios similar.

WINGS: dimensions 1.7 x 0.7; CuAx ratio: 0.8.

ABDOMEN: metallic green with short dark setulae; hypopygium as in Fig. 11; epandrial lobes arise internally, not visible in lateral view; hypandrium with ventral thorn-like projections at $\frac{5}{6}$, and apical comb-like projections; aedeagus expanded distally, with deep apicoventral notch; dorsal surstylar arm blunt, with apex curved mediad; distolateral cercal arm with strong dorsal setae along entire length.

FEMALE: unknown.

Remarks. *Corindia torresiana* and *C. capricornis* are probably sister species.

Corindia cooloola n. sp.

Type material. HOLOTYPE, ♂; PARATYPES 1♂♂, 3♀♀: Queensland: Cooloola National Park, on trunks *Eucalyptus* sp., 27 to 28-xi-1985, leg. D.J. Bickel (AMS).

Description. MALE: length 1.5–1.6; similar to *C. collessi* except as noted.

HEAD: vertex and frons metallic green with brown

pruinosity; face metallic blue-green.

THORAX: lateral scutellars reduced to tiny weak hairs.

LEGS: coxa I yellowish; coxae II and III brown basally but becoming paler distally; femora yellow to infuscated (femur III often brownish); remainder of legs yellow.

WINGS: dimensions 1.4 x 0.7.

ABDOMEN: hypopygium as in Fig. 16; hypandrium elongate, with flexion and sharp ventral protuberances at $\frac{5}{6}$, and with coarse apical serrations; aedeagus expanded distally, with deep apicoventral notch; ventral surstylar arm with internal median pedunculate seta, and with apical setae as figured; dorsal surstylar arm elongate, bare and with curved apex; distolateral arm of cercus elongate, mostly bare but with some apical setae.

FEMALE: similar to male; abdomen unicolorous metallic green.

Remarks. *Corindia cooloola* is known only from the type locality in coastal south-eastern Queensland. This species is similar to *C. capricornis* and *C. torresiana* in hypopygial structure, and the three species appear to be closely related.

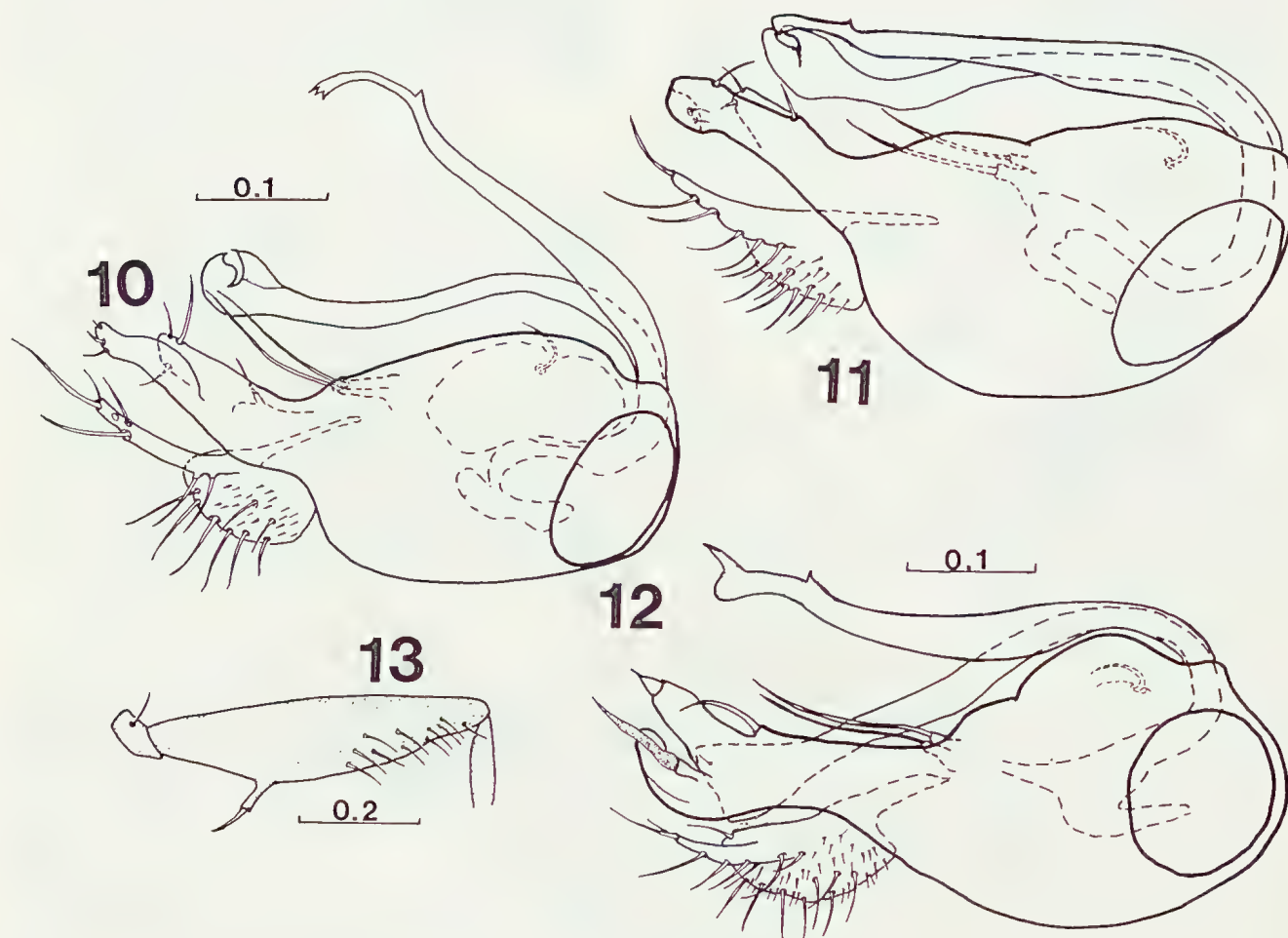


Plate III

Fig. 10. *Corindia capricornis*, Millstream, WA. Hypopygium, left lateral view.

Fig. 11. *Corindia torresiana*, Banks Island, Qld. Hypopygium, left lateral view.

Figs 12–13. *Corindia trudis*, Putty Rd., NSW. 12, Hypopygium, left lateral. 13, Male left leg III, anterior view.

Corindia nigricornis n. sp.

Type material. HOLOTYPE ♂; PARATYPES 9♂♂, 6♀♀: New South Wales: Myall Lakes National Park, on trunks *Angophora costata* and *Eucalyptus* sp., 21-xi-1985, leg. D.J. Bickel (holotype AMS, paratypes AMS, ANIC).

Additional material examined. 2♂♂, 5♀♀: Queensland: Cooloola National Park, on *Eucalyptus* sp., 27-xi-1985 (AMS).

Description. MALE: length 1.9–2.0; similar to *C. collessi* except as noted.

HEAD: vertex, frons metallic green with grey-brown pruinosity; face shining metallic blue-violet with faint longitudinal furrows and some grey pruinosity; clypeus dark metallic green with brownish pruinosity; antenna entirely black.

THORAX: metallic blue-green with brownish pruinosity; setae yellowish; lateral scutellars about ¼ length of medians.

LEGS: coxae brownish basally, becoming yellowish distally; femora brown on basal ⅔; femoral 'knees' and remainder of legs yellow although tibia III infuscated on some specimens.

WINGS: dimensions 1.5 x 0.6; CuAx ratio: 0.6; M arches anteriorly somewhat, almost similar to M curvature in *Medetera*; lower calypter with yellow setae and halter pale yellow.

ABDOMEN: dark brown; hypopygium shining dark brown with yellowish cercus (Fig. 14); hypandrium trough-like and expanded subapically, but without flexion or ventral thorn-like projections; aedeagus with subapical notch; surstylus with distinctive subapical cuticular hook; distolateral arm of cercus relatively short, with some dorsal setae and with strong apical seta as figured.

FEMALE: similar to male except lateral areas of abdominal terga 2 often yellowish.

Remarks. *Corindia nigricornis* is distinguished by black antennae, absence of a hypandrial flexion, and a hook-shaped surstylar arm. This species is found in coastal dry sclerophyll forests from southern Queensland to central New South Wales. At Myall Lakes, loose groups of 3–4 individuals would tend to line up behind each other on the tree trunks. A number of the specimens have reddish legs and abdominal pleural membranes, possibly the result of feeding on tiny red mites (some *Medetera*, which have been observed to feed on red mites, develop a bright red haemolymph which is similarly visible beneath pale cuticle and membrane).

Corindia robensis n. sp.

Type material. HOLOTYPE ♂: South Australia: Little Dip Conservation Park, 10 km S of Robe, 31-i to 4-ii-1978, leg. P.J.M. Greenslade (SAM).

Description. MALE: length 1.5; similar to *C. collessi* except as noted.

HEAD: antenna entirely black.

LEGS: coxae brown; femora dark brown, but femoral

'knees' yellowish; tibia I yellow but tibiae II and III and tarsomeres brown.

WINGS: dimensions 1.3 x 0.6.

ABDOMEN: dark metallic green; hypopygium dark brown (Fig. 15); hypandrium elongate, with ventral thorn-like projections at ⅓; aedeagus with apical notch; surstylus with distinctive dorsoapical clavate projection, with ventroapical knob-like projection bearing long curved seta and strong hooked dorsal seta; distolateral arm of cercus elongate and bare except for apical setae as figured.

FEMALE: unknown.

Remarks. *C. robensis* is known only from the type locality in south-eastern South Australia.

Corindia trudis n.sp.

Type material. HOLOTYPE ♂: New South Wales: Putty Road at Tinda Creek, 20 km N of Colo Heights, 17-ii-1984, on trunk *Eucalyptus haemastoma*, leg. D.J. Bickel (AMS).

Description. MALE: length 1.8; similar to *C. collessi* except as noted.

HEAD: face metallic blue with green reflections; scape and pedicel brownish; 1st flagellomere black.

THORAX: setae black.

LEGS: entirely dark brown, femoral 'knees' somewhat paler; podomere ratios similar; femur III with dark ventral cuticular projection at ⅓, bearing a pale tapering seta (Fig. 13).

WINGS: dimensions 1.7 x 0.7; CuAx ratio: 0.6.

ABDOMEN: metallic bronze-green with short dark setulae; hypopygium as in Fig. 12; hypandrium in lateral view with sharp ventral thorns at ⅓, and with a pointed ventroapical projection; aedeagus expanded apically with deep ventroapical cleft; surstylus with two stout apical arms separated by V-shaped gap; striated blade-like seta on pedicel arises from gap; ventral surstylar arm capped by stout conical seta, and subtended along ventral margin by strong curved seta.

FEMALE: unknown.

Remarks. The specific name, *trudis*, from the Latin meaning a pointed pole or pike, refers to the ventral projection of femur III. This projection is probably a secondary sexual character found only in males.

Genus *Thrypticus* Gerstäcker

Thrypticus Gerstäcker, 1864: 43. Type species *Thrypticus smaragdinus* Gerstäcker, by monotypy.

Diagnosis. Body colouration usually bright metallic green; eyes with short hairs between facets; only 1 sa present; coxa III with 2 lateral setae; femur II with strong posterior subapical seta; veins R_4+5 and M parallel to apex; CuAx ratio usually < 0.5, i.e., m-cu somewhat distant from posterior margin of wing; anal vein absent; hypandrium arising basoventrally from epandrium, and usually with a flexion or indentation in distal ⅓; hypopygial foramen left basolateral; aedeagus usually bifurcate apically; epandrial seta

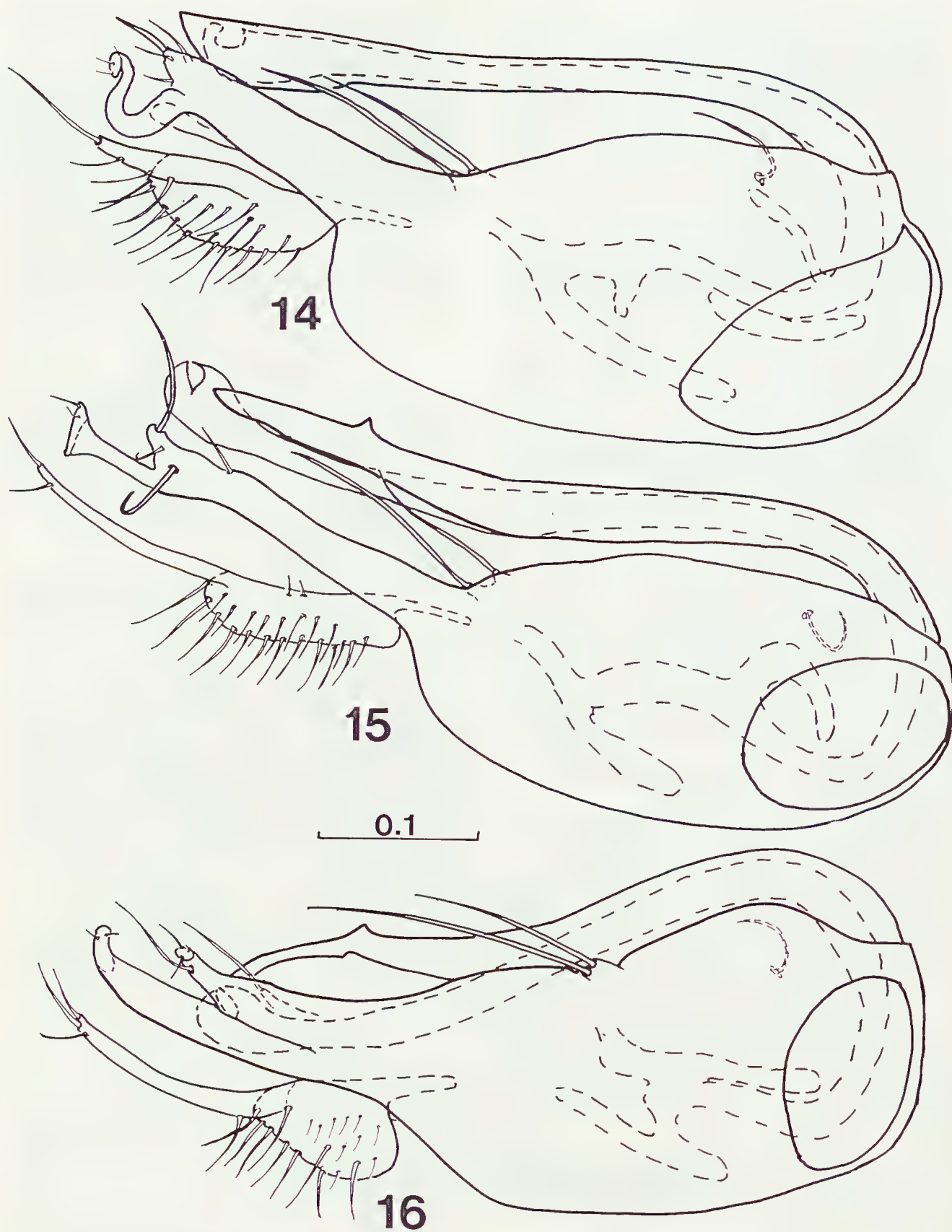


Plate IV

Fig. 14. *Corindia nigricornis*, Myall Lakes, NSW. Hypopygium, left lateral view.

Fig. 15. *Corindia robensis*, Robe, SA. Hypopygium, left lateral view.

Fig. 16. *Corindia cooloola*, Cooloola, Qld. Hypopygium, left lateral view.

strong, curved, internal, not visible in lateral view; epandrial lobes fused into elongate collar from which 2 bristles arise; surstylus strongly deflexed dorsad, usually lying conformably with similarly deflexed oblong-shaped cerci; cerci without distolateral arms; female oviscapt blade-like, sclerotized, narrow in dorsal view.

Remarks. *Thrypticus* is unique among the Dolichopodidae in that all known larvae are phytophagous stem-miners in the monocot families Cyperaceae, Graminae and Juncaceae (Dyde, 1959). Females have a sclerotized, blade-like oviscapt (Figs 23, 24) designed for piercing and ovipositing within stems. The relatively small adults are generally taken in wet grassland or marsh habitat.

Thrypticus australis n. sp.

Type material. HOLOTYPE ♂; PARATYPES 9 ♂♂, 8 ♀♀: **Australian Capital Territory:** Black Mountain Reserve, 22-ii to 29-iii-1968, I.B.F. Common (ANIC).

Additional material examined. **Australian Capital Territory:** Mt Majura, 2-iv-1963; Mt Coree, 13-iv-1968; Canberra, 7-x-1930, 22-ix-1930. **New South Wales:** 113 km W by S of Cobar, 10-xii-1982; Kincumber, SW of Terrigal, 8-xii-1976; 42 km NE of Deniliquin, 2-v-1978; Back Yama State Forest, 11-xi-1964; 20 km E of Forbes, in Callitris forest, 9-iv-1977; 55 km N of Mildura, 27-iii-1975; Ulladulla Beach, 1-x-1971; Lachlan River, 15 km SW of Euabalong, 28-xii-1976; The Rock, 14-ix-1968; 4.8 km S of Kiola, 3-x-1971; Fowlers Gap Reserve Stn, 31°05'S, 141°42'E, 29-xi to 2-xii-1981; Tumut Plains, 21-ix-1973; Ponds Creek, E of Armidale, 13-x-1962; Darling River, S of Bourke, 26-xii-1976; Colo Vale, 15-iii-1957 (USNM). **Norfolk Island:** Mt Bates, 300 m, 8-vi-1984. **Northern Territory:** 12 km SW of Alroy Downs, 10-iv-1976. **Queensland:** Boulter, 25 km NW by W of Birdsville, 8-iv-1976, at light; Lake Dynevor, 3-iii-1963, light trap. **South Australia:** Mungeranie Bore, 67.6 km N of Cooper's Creek, 17-ix-1972; Oratunga Creek, 11 km E of Parachilna, 4-x-1975; Germaine Gorge, 28-i-1959 (SAM); Muloorina Stn, 19-ii-1958 (SAM); Frome River Crossing of Cooper's Creek nr Marree, 26-x-1966 (SAM). **Tasmania:** Evandale, 1-iii-1967. **Victoria:** Lake Cullulleraine, 26-xii-1966; Cobran, 24-xii-1966; Glenelg River, 10-x-1962; Apollo Bay, 1-i-1967; 15 km S of Yarrora, 18-x-1983; Ovens River, E of Yarrawonga, 24-xii-1966; 13 km S of Pirita, 18-x-1983; Ouyen, 24-ii-1964 (MVM); Latrobe River Survey, Stn 10, 12, 20B, 24 to 31-x-1973 (MVM); 7 km SE of Hattah, 26-x-1966. **Western Australia:** Millstream, 10-iv-1971, 25-x-1970; Junana Rock, 26-x-1977, at light (female only). (217 specimens examined, all ANIC except where noted)

Description. MALE: length 1.3–1.4.

HEAD: vertex, frons, face dark metallic green with blue-violet reflections, and dusting of grey pruinosity; palpi and proboscis brown; antenna brown; scape short, with distal ring of setae; 1st flagellomere short, subrectangular, arista apical; dorsal postcranium strongly concave.

THORAX: bright metallic green with dusting of grey pruinosity dorsally, and with silvery pruinosity on pleura below notopleural suture; setae yellow; 5–6 pairs weak ac, about as long as width of ac band; 5 strong dc,

decreasing anteriorly; 1 pa, only 1 sa, 1 hm, 1 pm, 1 sr, 2 npl present; only median scutellars present, laterals absent; 1 propleural present.

LEGS: setae pale yellow; coxae metallic green; trochanters yellow; femora dark green to $\frac{3}{4}$; femoral 'knees', tibiae, basal tarsomeres yellowish; distal tarsomeres darkened; coxa II with lateral bristle; coxa III with 2 lateral bristles; relative podomere ratio: I: 3.1; 3.0; 1.4/0.7/0.5/0.3/0.5. II: 3.2; 3.1; 1.5/1.0/0.6/0.5/0.5; femur II with strong posterior subapical; tibia II with 1 ad at $\frac{1}{3}$ and strong ventral apical; III: 4.0; 4.0; 1.2/1.4/0.8/0.6/0.5.

WINGS: 1.3 x 0.5; $R_4 + s$ and M parallel to apex; m-cu at right angle to CuA; CuAx ratio: 0.4; lower calypter pale yellow, setae pale; halteres yellow.

ABDOMEN: bright metallic green with pale setulae, little pruinosity; abdominal terga 2–5 with 3–4 ovate depressions along lateral margins; relatively small sternum 8 covers left basal hypopygial foramen; hypopygium dark metallic green, appendages brownish (Fig. 17); epandrium pyriform, wide basally, narrowed distally, with dorsally deflexed lobate surstyli and conformably lying cerci; hypandrium arising basoventrally, with distinct flexion at about $\frac{2}{3}$; hypandrium beyond flexion triangular, broad basally and tapering distally, heavily melanized (Fig. 18); aedeagus arising from base of epandrium, apically cleft; strong epandrial seta arising from lateral walls of genital chamber, not visible externally; epandrial lobes fused into elongate collar, bearing 2 strong bristles distally; surstylus lobate, distally melanized, with strong ventral seta at $\frac{2}{3}$, and 2 short distal setae; cercus sparsely haired apical section.

FEMALE: similar to male except where noted.

HEAD: face slightly wider than male.

ABDOMEN: segment 7 (forming the oviscapt sheath) black, glabrous; oviscapt (Figs 23, 24) blade-like, distally dark brown with paler branched median tract, and with irregular margins as figured.

Remarks. Becker (1922:54) described *Thrypticus abditus* from a syntypic pair, a male from New South Wales (deposited at the Hungarian National Museum) and a female from Taiwan (deposited at Institut für Pflanzenschutzforschung, Eberswalde-Finow, DDR). The male syntype has since been destroyed, thus the female alone carries the species name and is regarded as the lectotype. There can be little doubt that the male was a specimen of the widespread Australian species considered above. However, female *Thrypticus* rarely bear discernable species-specific characters which enable them to be accurately associated with males of their species, or to be distinguished from other female *Thrypticus* species. In fact, the association of males and females of varied species from the same locality is often problematical. Although some dolichopodid species do have wide ranges which encompass both Taiwan and Australia (e.g., *Medetera grisescens*, *Megistostylus longicornis*), and some *Thrypticus* species are widespread [e.g., *T. fraterculus*, in North and South

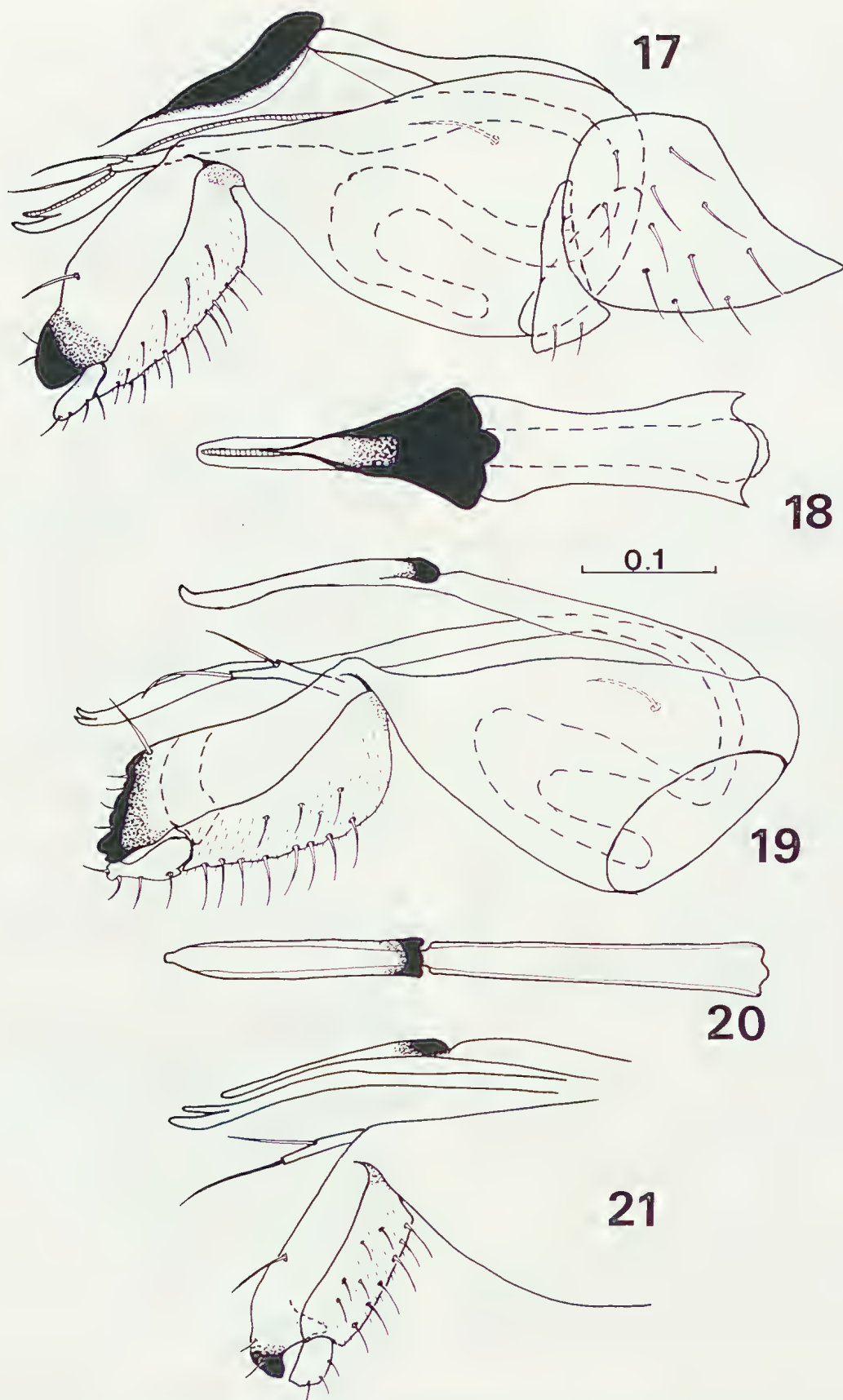


Plate V

Figs 17-18. *Thrypticus australis*, Black Mtn, ACT. 17, Hypopygium, left lateral. 18, Hypandrium and aedeagus, ventral view.
 Figs 19-20. *Thrypticus tropicus*, near Mt Isa, Qld. 19, Hypopygium, left lateral. 20, Hypandrium, ventral view.
 Fig. 21. *Thrypticus sumatranus*, Fort de Kock, Sumatra, paratype. Hypopygium, distal, left lateral view.

America and possibly Siberia (Robinson, 1975), *T. bellus* across Eurasia], the only evidence for *T. abditus* having an Indo-Australian distribution is an unjustified association of isolated specimens. I have been unable to locate any other museum specimens of Taiwanese *Thrypticus* to verify the distribution. Therefore, I have designated a new Australian species, *Thrypticus australis*, and regard *T. abditus* as an Oriental species.

Thrypticus australis occupies a broad zone across much of Australia and is also present on isolated Norfolk Island, more than 1400 km from the eastern Australian coast (see map, Fig. 25). It has been taken from such diverse habitats as coastal beaches, montane and subalpine woodland, and interior desert. It is one of the few dolichopodids found almost throughout the semiarid and arid interior. Although species of *Hydrophorus* and *Thinophilus* are usually taken near saline playa lakes, *Thrypticus australis* seems more or less associated with riverine habitats and probably is able to utilize its unique larval stem-mining habit to exploit the temporary abundance of grasses after rainfall. Although nothing is known of the immature stages of *T. australis*, its life history in the arid interior would make an interesting ecological study.

Apart from body size, intraspecific variation in *T. australis* includes a tendency for infuscated tibiae, especially tibia III, in specimens from Victoria and Tasmania, and a varying extent of melanization on the hypandrium.

Thrypticus tropicus n. sp.

Type material. HOLOTYPE ♂; PARATYPES 1 ♂, 1 ♀: **Queensland:** Big Mitchell Creek, Mareeba-Molloy Road, 4-v-1967, leg. D.H. Colless. PARATYPE 1 ♂: 66 km NW of Mt Isa, 9-iv-1976, at light (ANIC).

Description. MALE: length 1.3–1.4; wing 1.1 x 0.5; similar in almost all respects to *T. australis* except as noted: tibiae paler yellow; CuAx ratio: 0.45.

ABDOMEN: hypopygium as in Fig. 19; hypandrium beyond flexion parallel-sided, with only slight basal melanization (Fig. 20); epandrial lobes fused, with bristles as figured; aedeagus projecting to apex of surstylus; surstylus prolonged along dorsal side, distally melanized, with strong subapical ventral seta, 3–4 distal short setae, and median process projecting down towards cercus; cercus lying conformably with dorsal margin of surstylus, with distinct apical section bearing only 3 setae.

FEMALE: similar to female *T. australis*.

Remarks. *Thrypticus tropicus* is known from two localities in tropical northern Queensland.

Thrypticus fortescuensis n. sp.

Type material. HOLOTYPE ♂; PARATYPES 3 ♂♂: **Western Australia:** Millstream, 25-x-1970, leg. D.H. Colless (ANIC).

Description. MALE: length 1.4–1.5; wing: 1.2 x 0.5;

similar in almost all respects to *T. australis* except as noted: body colour a darker blue-green in all specimens; CuAx ratio: 0.4.

ABDOMEN: hypopygium as in Fig. 22; hypandrium parallel-sided, similar to that of *T. tropicus* (Fig. 20); surstylus elongated, subequal in length to epandrium, aedeagus thus only extending $\frac{2}{3}$ length surstylus, not reaching distal margin; surstylus with strong ventral seta at $\frac{2}{3}$, somewhat expanded, and strongly melanized distad, with 2–3 apical setae.

FEMALE: unknown.

Remarks. This species is known only from the type series taken along the Fortescue River, Western Australia.

Discussion

Of the three new Australian species described here, *Thrypticus australis* is the most distinctive, with its wide distal triangular-shaped hypandrium, while *T. tropicus* and *T. fortescuensis* are less readily separated and seem close to the Oriental *T. sumatranus* and a number of palearctic species. I have examined the types of *T. sumatranus* (Hollis, 1964:258; ZMUA) and have figured the distal hypopygium (Fig. 21). Only rather slight details of the surstylus seem to separate a number of Old World species (also see figures in Negrobov, 1971–77), and a possibility remains that some of these species might represent local variants of more widespread polytypic species.

Thrypticus is almost cosmopolitan in distribution, with 71 described species: 39 from the New World, 4 afrotropical, 23 palearctic, 2 Oriental, and 3 new Australian species. The genus seems to have radiated extensively in the neotropics (see Robinson, 1975). From examination of descriptions and genitalic figures (especially Negrobov, 1971–77; also Robinson, 1975, 1980), it is possible to define at least the palearctic species groups and place the Australian species within that context.

1. The *smaragdinus* group: this species group contains a single European species, *T. smaragdinus*, and although the type of the genus, it is rather unrepresentative. It has the following features: tapering hypandrium without flexion; aedeagus without apical cleft; abundant setae on surstyli; 3–4 pairs scutellars; oviscapt with ventral projection; face in both sexes very long; large body size, > 2.8 mm.

2. The *bellus* group: this species group includes 22 of the 23 palearctic *Thrypticus* species considered by Negrobov: *T. bellus*, *T. atomus*, *T. viridus*, *T. incanus*, *T. pollinosus*, *T. vestis*, *T. paludicola*, *T. intercedens*, *T. emilae*, *T. cuneatus*, *T. nigricauda*, *T. fennicus*, *T. divisus*, *T. laetus*, *T. altaicus*, *T. virescens*, *T. politus*, *T. tarsalis*, *T. pruinosis*, *T. tsacasi*, *T. riparus* and *T. tonus*. In addition, at least the nearctic *T. willistoni* and *T. fosteri*, the New World and possibly palearctic *T. fraterculus*, the oriental *T. sumatranus* and probably *T. abditus*, and the three new Australian species, *T. australis*, *T. fortescuensis* and *T. tropicus* belong here

as well. The *bellus* group is characterized by: hypandrium with distinct flexion or pinched area at about $\frac{2}{3}$, with melanized thickening immediately distad; aedeagus with apical cleft; surstyli with only sparse distal setae; surstyli and cerci lying conformably together and usually strongly deflexed from long axis of epandrium; oviscapt without ventral projection; one pair of median scutellars present, the laterals as weak short hairs or lost; body length often < 2.0 .

A number of other species groups await delimitation, especially in the New World.

The clear association of the Indonesian *T. sumatranus* and the three new Australian species with the principally holarctic *bellus* group suggests a northern origin for the Australasian *Thrypticus* fauna. Although I have seen no *Thrypticus* from New Guinea or the Melanesian

archipelago, its presence there might be expected. *Thrypticus australis* at least has been able to reach Norfolk Island. A species of *Thrypticus* described from New Zealand belongs to a different genus (see Appendix) and probably *Thrypticus* is absent from New Zealand.

Phylogenetic Analysis

I have presented a cladistic analysis of the Medeterinae (Bickel, 1985) in which *Thrypticus* was regarded as derived from *Medetera*. However, study of *Corindia* has led me to alter these conclusions and following is a revised analysis. Also included in the analysis is the palearctic genus *Dolichophorus*.

The first 18 characters and their character states were

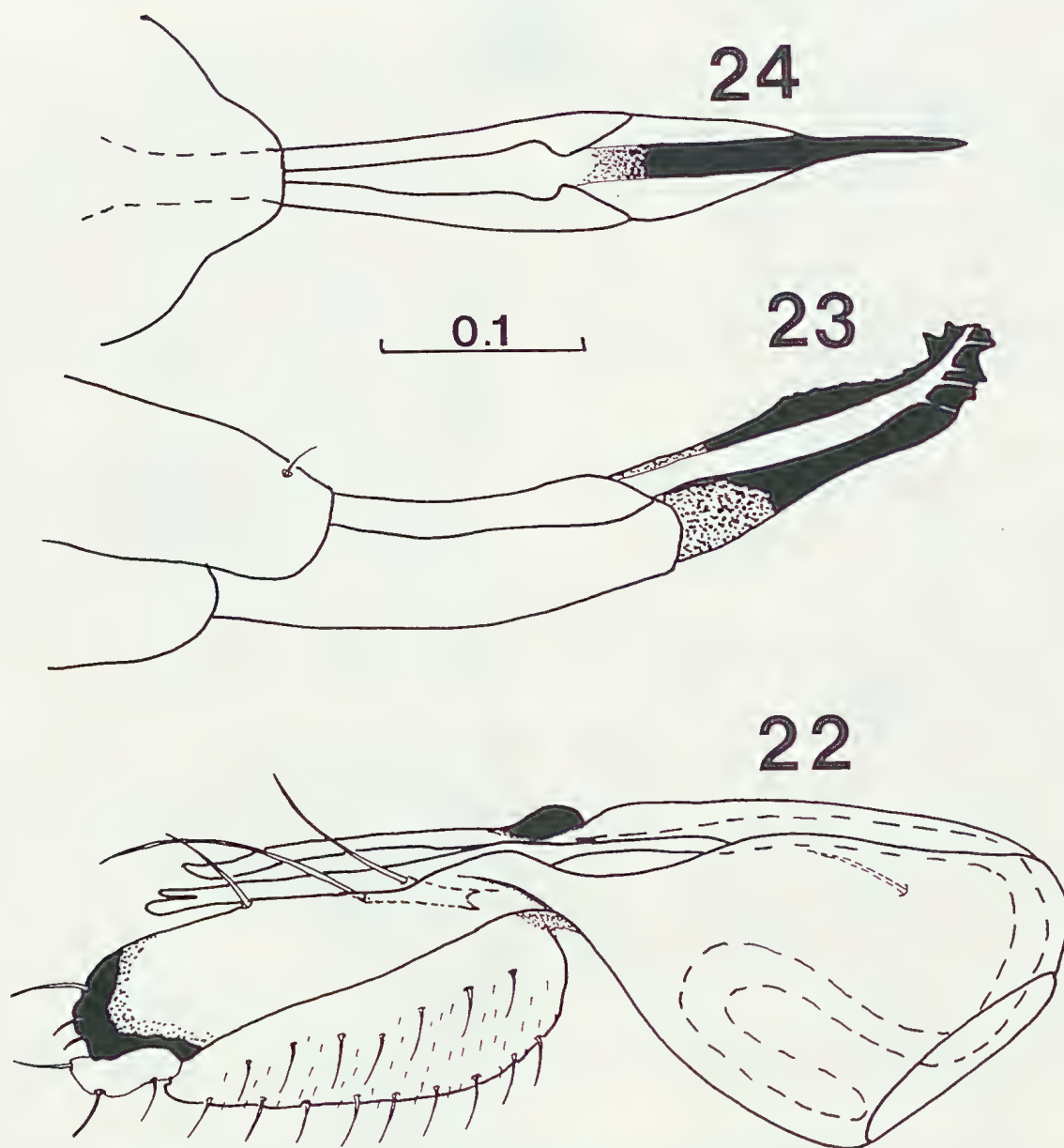


Plate VI

Fig. 22. *Thrypticus fortescuensis*, Millstream, WA. Hypopygium, left lateral view.

Figs 23-24. *Thrypticus australis*, female terminalia: 23, left lateral view. 24, Dorsal view.

discussed in Bickel (1985) and will be summarized in the following format — Character: plesiomorphic (ancestral) state/ apomorphic (derived) state.

1. Vestiture of eyes: short hairs present/ bare.
2. Postcranium: convex or flat dorsally/ concave dorsally.
3. Proboscis: weakly sclerotized/ massive, heavily sclerotized.
4. Lateral scutellars: strong bristles/ reduced to short hairs or lost.
5. Mesoscutal slope: convex/ flattened.
6. Anterior preapical femorals on II, III: present/ absent.
7. Strong anterolateral bristle on coxa I: absent/ present.
8. Coxa III lateral bristles: one/ two.
9. Male tarsus I: unmodified/ lobate tarsomeres.
10. Anal vein: present/ reduced or lost.
11. *Bosse alaire*, the flexion in vein M: present/ lost.
12. Hypopygium: encapsulated at tip of abdomen/ pedunculate.

13. Epandrial lobes: bases separate/ bases fused.

14. Attachment of surstyli to epandrium: suture line present/ fused with no suture evident.

15. Relative length of ventral and dorsal surstyli: subequal/ dorsal lobe longer.

16. Cercus: undifferentiated/ with strong projecting distolateral arm.

17. Female oviscapt: broad, with dorsal dornen or setae/ narrow, blade-like, heavily sclerotized.

18. Larva: subcortical predators/ grass stem-miners.

19. Distal sectors of veins M and R_4+5 : straight, subparallel to apex/ arched anteriorly, converging somewhat. I had previously considered that *Thrypticus* had undergone a character reversal to regain the plesiomorphic state from the apomorphic, *Medetera*-type venation. I no longer regard *Thrypticus* as derived from *Medetera*, and the venation of *Thrypticus* and *Corindia* should be regarded as plesiomorphic, similar to that of other dolichopodid subfamilies such as the Sympycninae and Diaphorinae.



Plate VII

Fig. 25. Distribution Map of Australian *Thrypticus*.

- *T. australis*
- *T. australis* (?), female only.
- ▲ *T. tropicus*
- *T. fortescuensis*

20. Supraalar bristles (sa): two/ one, the anterior bristle lost. I regard 2 sa as part of the ground-plan for the Dolichopodidae. In most *Medetera*, 2 sa are present, although the anterior bristle is generally about $\frac{1}{2}$ the size of the posterior. In *Corindia*, *Thrypticus*, *Dolichophorus*, and a few species of *Medetera*, the anterior bristle is lost; a derived state.

21. Femur II posterior subapical bristle: present/ absent. The presence of this bristle is regarded as part of the dolichopodid groundplan. This bristle is present in both *Corindia* and *Thrypticus*, but absent in *Medetera* and *Dolichophorus*.

22. Hypandrium, attachment to epandrium: basal/ mid-

ventral. The hypandrium arises from the base of the epandrium in most Sympycninae and Diaphorinae and is tentatively regarded as the plesiomorphic condition. Expansion of the basal epandrium and/or distal migration of the hypandrium would therefore be regarded as derived. The derived state is seen here in *Medetera* and *Dolichophorus*.

23. Position of the hypopygial foramen: left basolateral/ left mid-dorsolateral. Similarly, the hypopygial foramen is distinctly basolateral in the Sympycninae and Diaphorinae and is regarded as the plesiomorphic condition. The distal migration of both the hypopygial foramen and the hypandrium-epandrium attachment

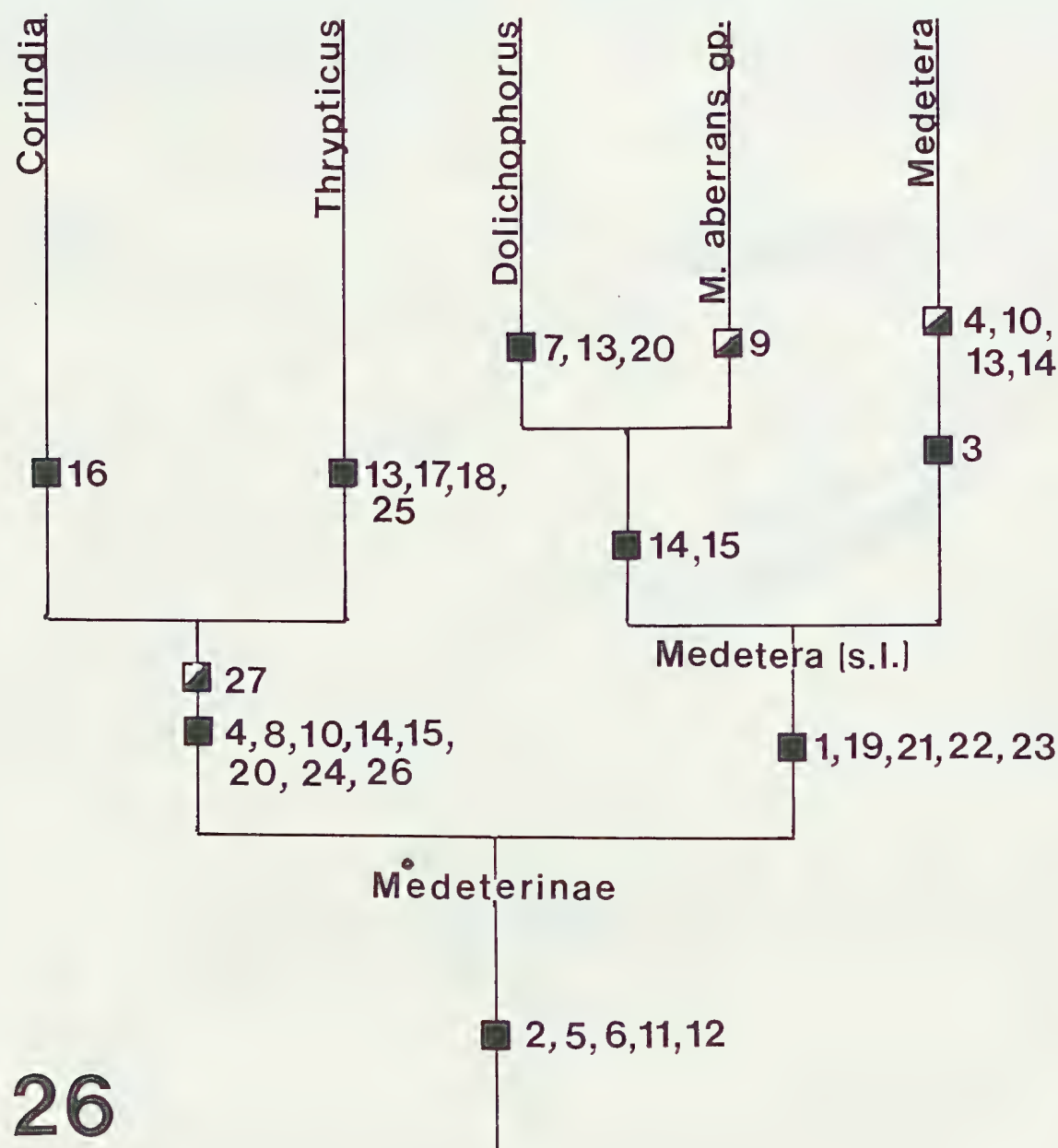


Plate VIII

Fig. 26. Cladogram of Medeterine Genera. Numbers refer to characters discussed in text.

■ Apomorphy

◐ Apomorphy shared by only some members of group.

(22) may be related phenomena, occurring simultaneously with hypopygial modification. *Medetera* and *Dolichophorus* display the derived condition.

24. Epandrial seta: straight, external, arising along ventral margin of epandrium, usually visible laterally/curved, internal, arising from lateral wall of epandrial chamber. The derived condition is found in both *Corindia* and *Thrypticus*.

25. Position of cerci and surstyli: cerci free and not conforming to shape of surstyli/ cerci lying conformably along dorsal margin of surstyli. In *Thrypticus*, both the cerci and surstyli are distally deflexed and lie conformably together.

26. Apex of aedeagus: simple/ cleft, or notched. *Thrypticus* and *Corindia* both display the derived condition; *Thrypticus* with a bifurcate cleft apex, *Corindia* with a deep apicoventral notch.

27. Flexion of hypandrium: absent/ present. Almost all *Corindia* and at least the *bellus* species group of *Thrypticus* have a distinct flexion or narrowed pinched portion in the distal third of the hypandrium. This is considered a derived character and is possibly a synapomorphy for the two genera with secondary loss in some *Thrypticus* species groups.

A cladogram representing the relationships of *Corindia*, *Thrypticus*, *Dolichophorus*, *Medetera* and the *Medetera* 'aberrans species group' is presented in Figure 26. *Corindia* + *Thrypticus* share strong synapomorphies 8, 24 and 26, and the somewhat weaker synapomorphies 4, 10, 15 and 20 which are homoplastic within *Medetera*. Derived character 27 may also be a synapomorphy for the *Corindia* + *Thrypticus* although it is not always developed in the two genera. *Thrypticus* is strongly defined by autapomorphies 13, 17, 18 and 25. *Corindia* is defined by autapomorphy 16, which also occurs in some *Medetera*, although perhaps not strictly homologous.

Medetera (s.l.) is defined by strong synapomorphies 1, 19, 21, 22 and 23. *Dolichophorus*, a palearctic genus of two species, is considered the sister taxon of the *Medetera* 'aberrans species group'. The phylogenetic relationships of *Medetera* are treated in greater detail in Bickel (1985) and in a revision of the Indo-Australian fauna currently in preparation.

Corindia and *Thrypticus* are regarded as having a sister group relationship. Both genera have a similar habitus and hypopygial morphology. Of the two genera, *Corindia* has a more generalized oviscapt, while *Thrypticus* has evolved into a new adaptive zone, with a highly specialized oviscapt designed for piercing the stems of grass-like monocots, where its larvae develop as phytophagous miners. *Thrypticus* probably evolved from a *Corindia*-like ancestor, although most certainly outside the Australian region. The apparent confinement of *Corindia* to Australia may reflect the relict distribution of a once more widespread taxon.

D.H. Colless (ANIC); A. Neboiss (MVM); L. Queale (SAM); and F.C. Thompson (USNM). B. Holloway (NZAC) and P. Oosterbroek (ZMUA) generously lent type material.

References

- Becker, T., 1922. Dipterologische Studien, Dolichopodidae der indo-australischen Region. *Capita Zoologica* 1(4):1-247.
- Bickel, D.J., 1985. A revision of the Nearctic *Medetera* (Diptera: Dolichopodidae). United States Department of Agriculture Technical Bulletin 1692: 1-109.
- Cregan, M.B., 1941. Generic relationships of the Dolichopodidae based on a study of the mouthparts. *Illinois Biological Monographs* 18: 1-68.
- Dyte, C.E., 1959. Some interesting habitats of larval Dolichopodidae (Diptera). *Entomologist's Monthly Magazine* 95: 139-143.
- Gerstcker, A., 1864. Uebersicht der in der Umgegend Berlins bis jetzt beobachteten Dolichopodiden. *Stettiner Entomologische Zeitung* 25: 20-48.
- Hollis, D., 1964. Notes and descriptions of Indonesian Dolichopodidae in the Zoologisch Museum, Amsterdam. *Beaufortia* 10: 239-274.
- McAlpine, J.F., 1981. Morphology and terminology - adults. In J.F. McAlpine et al., 'Manual of Nearctic Diptera' Vol. 1: 9-64. Research Branch Agriculture Canada, Monograph 27, Ottawa, 674 pp.
- Negrobob, O.P., 1971-1977. Dolichopodidae, Unterfamilie Medeterinae. In 'Die Fliegen der palaearktischen Region' (E. Lindner, ed.) 29: 269-353, Lieferungen 284 (1971), 289 (1972), 302 (1974), 303 (1974), 316 (1977). Schweizerbart, Stuttgart.
- Parent, O., 1933. tude monographique sur les Diptères Dolichopodides de Nouvelle Zlande. *Annales de la Socit scientifique de Bruxelles (B)* 53: 323-441.
- Robinson, H., 1975. Bredin-Archbold-Smithsonian Biological Survey of Dominica. The family Dolichopodidae with some related Antillean and Panamanian species (Diptera). *Smithsonian Contributions to Zoology* 185: 1-141.
- Robinson, H., 1980. Three new species of *Thrypticus* from Maryland (Diptera: Dolichopodidae). *Proceedings of the Entomological Society of Washington* 82: 469-473.

Appendix

Parent (1933:361) described *Thrypticus nigrichaetus* from a single female taken at Otira, New Zealand. I have examined the holotype (NZAC) which has the head, left wing, and left legs I, II and III missing. The specimen is obviously not a *Thrypticus* since it bears the following features in contrast with typical *Thrypticus*: 2 sa, coxa III with only 1 lateral bristle, femora II and III with distinct anterior preapicals, and female oviscapt broad, with a crest of spines. I regard this specimen as a *Chrysotimus*, a genus well represented in the New Zealand fauna. Female *Thrypticus* and *Chrysotimus* might easily be confused while roughly sorting dolichopodids, but it is surprising that a worker as competent as Parent should have described the specimen as a *Thrypticus*. Therefore, *Thrypticus nigrichaetus* Parent should be regarded as *Chrysotimus nigrichaetus* (Parent) new combination.

Accepted 22 November 1985

ACKNOWLEDGEMENTS. I wish to thank the following individuals for the loan of specimens: D.K. McAlpine (AMS);

Paleaequor, a New Genus of Polychaete Worm (Chrysopetalidae)

CHARLOTTE WATSON RUSSELL

Department of Annelids, Natural Sciences,
Northern Territory Museum, GPO Box 4646,
Darwin, NT 5794, Australia

ABSTRACT. A new genus, *Paleaequor*, of the polychaete family Chrysopetalidae is described. Three new species: *Paleaequor setula*, the type species from north-eastern Australia; *P. psamathe* from western Mexico; and *P. nicoyensis* from the Pacific coast of Costa Rica, are described. Two previously described species, *Paleanotus heteroseta* Hartman, 1945 and *Bhawania brevis* Gallardo, 1968, are referred to the new genus. A key to the species of *Paleaequor* is provided and comparison between the Western Pacific and American species made.

WATSON RUSSELL, CHARLOTTE, 1986. *Paleaequor*, a new genus of polychaete worm (Chrysopetalidae). Records of the Australian Museum 38(3): 153–174.

Ehlers (1864) established the family Chrysopetalidae (as Chrysopetalea) to contain the new genus *Chrysopetalum* Ehlers, 1864; *Paleanotus* Schmarda, 1861; and *Bhawania* Schmarda, 1861. Levinsen (1879) later included his genus, *Dysponetus*, within the family.

While there has been some revision of individual genera and description of new chrysopetalid species (e.g. Jorge, 1954; Mileikovsky, 1962; Orensanz, 1972; Perkins, 1985) there has been no comprehensive revision of the family. The morphology of chrysopetalid species is poorly known. These worms are mostly small to very small in size, the anterior segments are retractile and difficult to study; and differences in setal structure and ornamentation can be observed only under high magnification. These may be some of the reasons why chrysopetalids have been often misidentified to genus and why widespread species have been placed into cosmopolitan species complexes.

Ongoing studies of the Chrysopetalidae by the author have established important generic differences which include degree of retraction of anterior segments; number, size and shape of appendages of the prostomium, peristomium and the first setigerous segment; presence of a caruncle or nuchal fold; form of the pygidium; and the number, type and ornamentation of setae. Identification to species is based

primarily on number, type, position and ornamentation of notosetae and neurosetae.

During this study large numbers of specimens, including some misidentified as *Bhawania* and *Paleanotus*, were examined and found to represent an undescribed genus and species. These are described herein as new and a new generic name is proposed. Two previously described species, *Paleanotus heteroseta* Hartman and *Bhawania brevis* Gallardo, also are referred to the new genus.

Materials and Methods

Material examined is deposited in the following institutions: Allan Hancock Foundation, University of Southern California, Los Angeles (AHF); Australian Museum, Sydney (AM); British Museum (Natural History), London (BMNH); California Academy of Sciences, San Francisco (CAS); Museum National d'Histoire Naturelle, Paris (MNHN); Northern Territory Museum, Darwin (NTM); Queensland Museum, Brisbane (QM); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM).

Length is measured from the tip of the most extended appendages or setae of the anterior segments to the tip

of the paleae that extend past the pygidium. Width is measured mid-body, at the widest point, from tip to tip of the most extended setae, i.e. neurosetae or paleae. Chrysopetalids are fragile, and twists in the body due to preservation often make it difficult to flatten the animal for mounting on a slide and measuring. Where sufficient entire specimens were present, individuals were broken mid-body to measure length and width, and a number of segments were mounted between two cover slips in order to distinguish accurately setal numbers and types in both dorsal and ventral view.

Jorge's (1954) method was used in investigating the number and position of appendages on the prostomium, peristomium and first and second setigers: anterior ends were mounted between two cover slips and separate drawings made of the dorsal and ventral aspects. If the anterior segments are half to fully retracted, it is difficult to interpret the number and position of appendages. When the anterior segments are relaxed the paleae fans of the second and third setigers can be gently removed and the prostomium, peristomium and first and second setigers should be clearly visible.

To elucidate setal change throughout the body, a number of entire specimens from each species was dissected segment by segment and each setal type counted. The numbers of paleae and neurosetae together with the rib counts of the former are given as a range. Rib counts may vary within the fan from one palea to the next. They may also vary on paleae between the anterior and posterior ends and from small to large individuals. In order to make a standard comparison, all counts herein were based on mid-body setigers, except where otherwise indicated. Rib counts are of the longitudinal ribs and were made at the widest part of the distal end of the palea. Raised ribs, which in some

specimens only extend one half to two thirds the length of the palea, were counted at the mid-palea.

Use of a Scanning Electron Microscope (SEM) revealed in detail certain structures. SEM photographs helped to clarify paleae ornamentation which included the presence of shallow raised ribs serrated with a longitudinal series of indented cusps; a degree of fine serration of both palea margins and the presence of a type of reticulated scale that can obscure the granular pattern on the superior surface of the palea (Fig. 18).

Parapodia were excised and subjected to 10–30 seconds in an ultrasonic cleaner prior to preparation for SEM study. Parapodia were successively placed for 5 minutes in 70% EtOH, 5 minutes in 85% EtOH, 5 minutes in 95% EtOH and 5 minutes in 100% EtOH. No adverse effects followed the omission of amyl acetate in the final preparation. Specimens were put into the critical point dryer and after this procedure positioned with a spot of glue on a cover slip. Specimens were coated with a thin carbon underlay then sputter coated with gold palladium alloy.

At the USNM, a Cambridge S4-40 SEM was used. This SEM when set for a 20kv beam gave better resolution at high magnifications (e.g. x 5000) than 10kv. At Macquarie University a JOEL SEM unit was used.

Terminology of Setal Fascicles

Chrysopetalid setae consist of a notopodial fascicle of flattened setae referred to as 'paleae' and a neuropodial fascicle of falcigers and/or spinigers. The composition and distribution of notosetal and neurosetal types, particularly the structure of the paleae and the composition of the paleae fan have been



Fig. 1. Distribution map of *Paleaequor* species.

elucidated with the use of SEM in the present study.

An attempt has been made to divide the noto- and neurosetal fascicles into the units that can be counted and categorized according to shape. It should be noted, however, that most of these categories (especially neurosetal) are not entirely discrete as the setal fascicles are composed of a series of gradations of form with some setae inevitably possessing intermediary characters.

NOTOSETAL CHARACTERS. Chrysopetalids possess a notopodium with a dorsal horizontal ridge, in which a fascicle of paleae inserts both above and below the dorsal aciculum.

Previous authors have variously described the components of the paleae fan as 'smaller, narrower, larger, broader' (Schmarda, 1861; Ehlers, 1864; Hartman, 1945; Gallardo, 1968). The paleae fan consists of three parts, and a description of the three parts of the paleae fan in *Paleaequor* species in this paper is based on position within the fan—'lateral' (small group of narrow paleae that insert below the dorsal aciculum and adjacent to the dorsal cirrus), 'main' (large group that insert mid position above the aciculum) and 'median' (small group most proximally located) (Fig. 7). Two groups of intermediate paleae are regarded and counted as two separate subunits. The first subunit is located in between the lateral and main paleae groups and is present on all setigers. The second subunit is located between the main and median groups and is present only in posterior setigers.

Lateral paleae. Lateral paleae are thin, pointed and lack raised ribs and granules (Fig. 15). The first and second notopodia possess modified paleae. These have margin serration to the apex and are broader and shorter than subsequent lateral paleae.

Main fan. The main fan is comprised of large, symmetrical paleae with a number of longitudinal internal and raised ribs and, on the superior surface, a granular ornamentation. The large main fan can be sub-divided into distal, mid and proximal groups (Fig. 7). The number of ribs of each palea varies within a small range, distally to proximally, within the main fan. In general the most distal paleae have fewer ribs and the mid to proximal paleae have a greater number of ribs (Tables 1, 3). *Paleaequor* species possess distally hyaline, erosive main paleae. The apex of these paleae appear to have undergone some structural weakening. Towards the distal quarter of the palea the horizontal striae fade, then disappear, leaving the longitudinal ribs to continue weakly to the apex. The finely serrate margins also discontinue towards the distal quarter which is composed of a flimsy, glassy tip, triangular in shape when entire and rounded or frayed when eroded (Fig. 18a,b).

Median paleae. A small group of median paleae of each parapodium interdigitates smoothly and flatly at the mid-body line. They are similar in shape to, and appear to be a continuation of, the main paleae fan but are nonetheless a discrete unit and insert at a shallow

angle to the main fan (Figs 13, 14). In general, the distal median paleae are larger, with rounded tips, and the proximal median paleae shorter, with rounded to pointed tips and a smaller hyaline apex. In some species the distal median paleae are very broad, with a large number of ribs, and in other species are less broad and have fewer ribs. The median paleae can be distinguished from the main paleae by having a more finely serrate proximal margin (Figs 22, 26).

Subunit 1. Subunit 1 consists of 2–3 slender paleae located in between the lateral and main groups and inserted just above the dorsal aciculum. The most distal subunit 1 palea is shorter and has fewer number of ribs compared to the more proximal palea (Fig. 15).

Subunit 2. The presence of a single, slender palea between the main and median groups, helps to delimit the main and median units. This small palea possesses equally serrate margins that continue nearly to the apex (Figs 22, 25). It is found only in the posterior body segments; in three species it is present only on the posterior ten setigers, and in two species on the posterior half of the body.

NEUROSETAL CHARACTERS. The neurosetal fascicle which inserts below the ventral aciculum is composed of spinigers and falcigers which are divided into four units based on position: superior spinigers; mid-superior falcigers; mid-inferior falcigers; and inferior spinigers or falcigers (Fig. 7). Two subunits are recognised.

Units 1 to 4. The first unit is composed of a small number of superior spinigers. The uppermost spinigers in this group have long blades while those in the lower position have slightly shorter blades with a greater degree of dentition. The second unit of mid-superior falcigers is composed of long-bladed falcigers in the uppermost position, and falcigers with medium length blades and very pronounced basal dentition in the lower position. The third unit has a large number of mid-inferior falcigers. The uppermost falcigers in this group have medium length blades with less pronounced dentition while those in the lower position have shorter blades and similar dentition. The small fourth unit comprises an inferior group of spinigers or falcigers according to species group. The inferior spinigers have short, attenuated blades with long, fine teeth and the inferior falcigers have short, broad to narrow blades, with short, fine to no dentition.

Subunits 1 and 2. The first subunit is an additional (or replacement) short spiniger located between the first and second units and present on posterior setigers in all species. The second subunit is a particularly narrow falcigerous seta located within the fourth unit, and is present on posterior setigers in three species.

Taxonomy

Family CHRYSOPETALIDAE Ehlers, 1864

Paleaequor n. gen.

Type species. *Paleaequor setula* n. sp.

Description. Body rectangular, narrow, slightly tapered at both ends. Juveniles elongate, ovoid shape. Maximum segment number 127. Body pale yellow to brown with reddish brown to brown pigmented patches on bases of dorsal and ventral cirri and pygidial lobe. Pale gold to golden brown paleae fans imbricate over dorsum, covering worm completely. Paleae in transverse row in notopodium with leading edges visible proximally; median paleae interlock in the midline forming gently convex to flattened dorsum. Anterior three segments in conjunction with prostomium largely retractable. Prostomium subrectangular, longer than wide, compressed between anterior segments. Two pairs of red-brown eyes arranged in rectangle on dorsal surface of prostomium, anterior pair larger. Single, subulate median antenna inserting anterior to anterior pair of eyes; two slightly longer lateral antennae inserting on anteroventral margin of prostomium. Two long, cylindrical palps inserting on ventral edge of prostomium. Horizontal, folded lip ventral and posterior to palps. Eversible proboscis with two fragile, transparent stylets. Semicircular glandular nuchal fold present posterior to prostomium. Peristomial or tentacular segment reduced, fused in part to prostomium; supporting a dorsal and ventral tentacular cirrus on each side, ventral pair originating adjacent to palps. First setigerous segment biramous, fused in part to peristomium. Notopodial fascicle with reduced numbers of paleae; neuropodium with fascicle of spinigerous neurosetae; dorsal cirrus present, ventral cirrus absent. Setigers two and three directed anterolaterally, all subsequent setigers laterally directed. All setigers except first with three types of paleae, dorsal and ventral cirri, and four types of spinigerous and falcigerous neurosetae. Interramal region ciliate. Notopodium with 3–8 slim, pointed lateral paleae with 3–8 ribs and very finely serrate margins, inserted posteriorly and overlying dorsal aciculum. Tiny, simple seta may also be present posterior to lateral group. 2–3 slender paleae (subunit 1) insert between the lateral and main groups, the most distal with 9–13 ribs, and shorter in length than proximal. The proximal with 12–15 ribs and 1 raised rib. Large group of symmetrical, broad main paleae with 15–24 ribs and 3–6 shallow, raised ribs. Proximal margin of main paleae more strongly serrate than distal margin. A single, slender palea (subunit 2), $\frac{1}{2}$ to $\frac{3}{4}$ length of main paleae inserting between main and median groups in the posterior half to posterior 10 setigers of body, and possessing 8–13 ribs, 1–2 raised ribs, and margins equally serrate. Median paleae, 2–4 in number, distinguished from main paleae by a weaker, more finely serrate proximal margin. Distal median paleae of same size, slightly or largely broader than main

paleae, with 16–26 ribs, 0–6 raised ribs. Next proximal median paleae shorter and more distally rounded with 13–21 ribs and most proximal paleae short, distally rounded to pointed with 8–20 ribs. Very fine to large, scattered to dense granular pattern present on superior surface of main and distal median paleae. Close-set horizontal striae in between longitudinal ribs fade towards distal tip of palea, leaving shallow, triangular, hyaline apex. Dorsal cirrostyle subulate, pseudoarticulated and retractile within cirrophore. Dorsal cirri longer on posterior setigers and extending past pygidium. Short to long, conical, pointed neuropodia not extending past notopodia and supporting a subacicular fascicle of heterogomph neurosetae. Superior group with 1–4 spinigers with long, slim shafts and long attenuated blades with fine basal dentition. One extra or replacement short spiniger (subunit 1) present within posterior setigers. Mid-superior group with 6–8 falcigers with long to medium length blades with coarse basal dentition. Mid-inferior group with 6–12 falcigers with medium to short length blades with less coarse basal dentition. Inferior group with 3–7 spinigers or falcigers with slim, short shafts and either narrow attenuated spinigerous blades with fine dentition or broad to narrow (subunit 2) falcigerous blades with fine to no dentition. All neurosetal shaft cores subdivided internally by longitudinal and horizontal striae. Ventral cirri slender, weakly pseudoarticulated and non retractile. Pygidium either quadrate with two anal cirri or rounded dorsally with two anal cirri and a small ventral cone. Anus ventral.

Remarks. *Paleaequor* differs from all other chrysopetalid genera in possessing two pygidial forms, finely ornamented paleae with erosive, hyaline tips, two inferior neurosetal forms and a wide range of neurosetal types including falcigers with prominent long toothed blades.

The formula of cirri on the anterior segments of *Paleaequor* is also found in two described and one undescribed chrysopetalid genera — *Bhawania* (unpub. data, author), *Paleanotus* (revision by author, in prep.) and n. gen. 1 (ms. in prep.). *Paleaequor* and *Paleanotus* are distinctly different genera with the former possessing greater body length and number of segments, greater degree of retractibility of the anterior segments and different numbers and types of notosetae and neurosetae. *Paleaequor* and *Bhawania* form a group within the Chrysopetalidae that possesses particularly retractile anterior segments, retractile dorsal cirri, and flattened golden brown paleae that cover the entire dorsum. *Paleaequor* most closely resembles *Bhawania* and has been previously confused with it. *Paleaequor* differs from *Bhawania* in possessing a narrower, shorter body with fewer number of segments. *Paleaequor* has a comparatively discrete, semicircular, glandular nuchal fold in comparison to the thick, fleshy, projecting nuchal ridge found in *Bhawania*. Both genera possess different pygidial forms and different numbers and types of notosetae and neurosetae.

Spinigerous inferior neurosetae have been reported for three species that have been incorrectly referred to *Bhawania* (*B. cryptocephala* Potts, 1910; *B. cryptocephala* var. *pottsiana* Horst, 1917; *B. pottsiana* Gibbs, 1971). These specimens exhibit characters that belong to both *Bhawania* and *Paleaequor* but until entire specimens can be examined the generic status of these chrysopetalids remains unclear.

Very little is known of the feeding biology of any chrysopetalid genera. The shape of the stylets is similar in all *Paleaequor* species and in comparison with other genera the only distinguishing feature in *Paleaequor* is the greater fragility and wider groove of the stylets. They also lack the serrated tips found in *Chrysopetalum* and *Paleanotus* (author, unpub. data). The function of the stylets interpreted from their structure would be one of piercing and sucking. *Paleaequor* has been recorded almost exclusively from sandy sediments, sometimes in association with large groups of tube-dwelling polychaetes (Wilson, 1979). It is possible that the *Paleaequor* species are omnivores feeding on small sand-dwelling invertebrates.

Paleaequor species are found in warm, tropical to subtropical waters between 37°N and 30°S (Fig. 1). They inhabit sediments that range from coarse sand and shell grit to fine sand and mud. Depth ranges from the intertidal to more than 80 m.

Etymology. The name *Paleaequor* is a combination of the Latin *palea*, meaning scale, and *aequor*, meaning an even, level surface, and refers to the flattened paleae that cover the entire dorsum. Gender neuter.

Key to *Paleaequor* Species

1. Pygidium quadrate without ventral cone (W. Pacific). 2
- Pygidium rounded with ventral cone (E. Pacific, W. Atlantic). 3
2. 4–8 lateral paleae; main paleae with 17–24 ribs; 4–5 inferior spinigers. *P. setula* n. sp.
- 3–4 lateral paleae; main paleae with 17–20 ribs; 5–7 inferior spinigers. *P. breve* (Gallardo)
3. Main paleae with 17–24 ribs; distal median paleae with 20–25 ribs. 4
- Main paleae with 17–19 ribs; distal median paleae with 16–20 ribs. *P. nicoyensis* n. sp.
4. Neurosetae with fine, short-bladed superior spinigers and 0–1 long-bladed mid-superior falcigers. *P. psamathe* n. sp.
- Neurosetae with robust, long-bladed superior spinigers and 2 long-bladed mid-superior falcigers. *P. heteroseta* (Hartman)

Paleaequor setula n. sp.

Figs 2–12

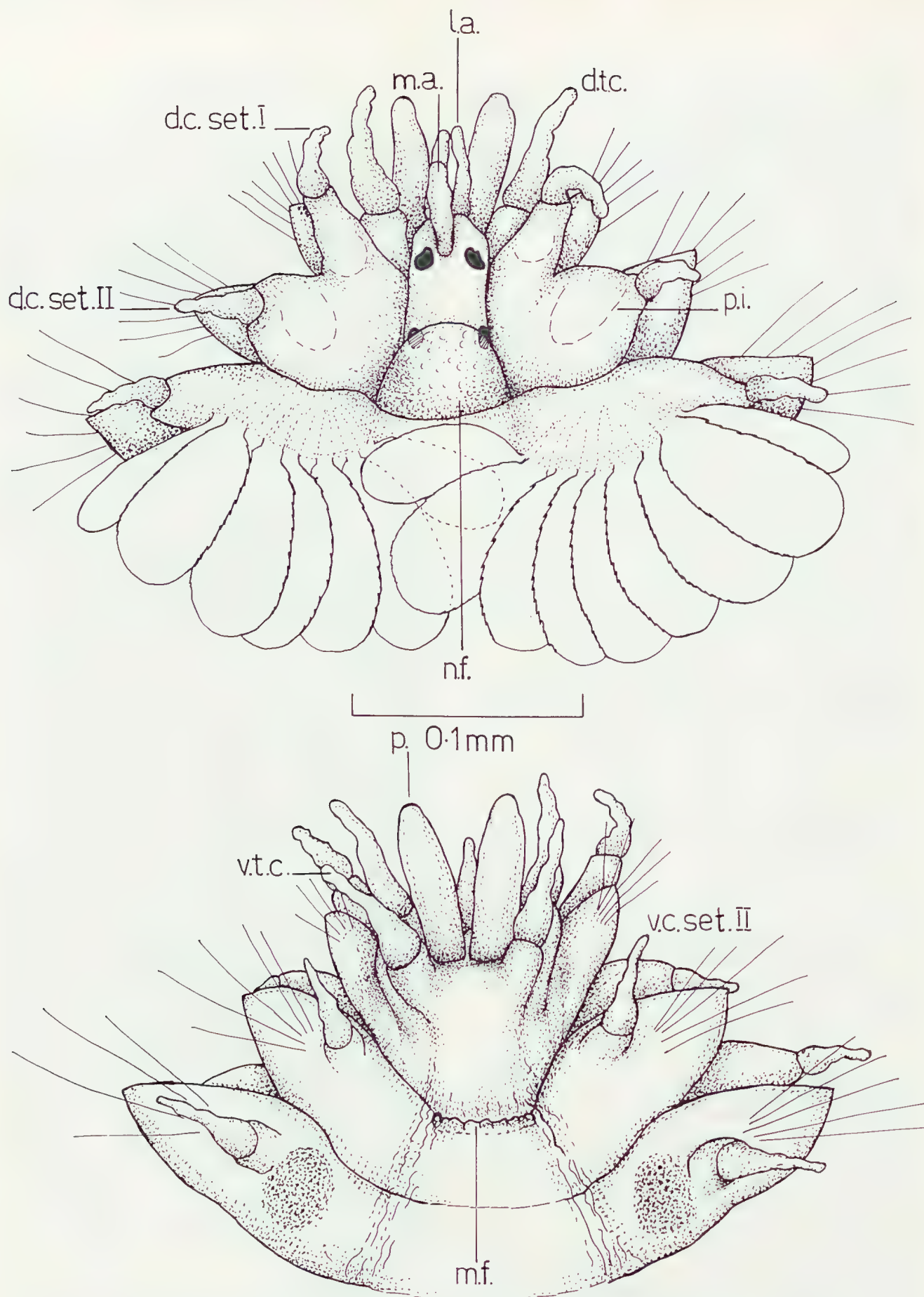
Material examined. HOLOTYPE: Australia, Queensland, Halifax Bay, Stn G (19°10'S, 146°44'E) slightly gravelly, muddy sand, 5 m, NTM W.1673, coll. J. Carey, January 1978; 68 setigers, 9.2 mm length, 1.2 mm width, specimen entire. PARATYPES: Queensland, Halifax Bay, Stn G, slightly gravelly, muddy sand, 5 m, 3, NTM W.1674, coll. J. Carey, January 1978; Halifax Bay, Stn E (19°09'S, 146°37'E), slightly gravelly, muddy sand, 5 m, 4, AM W. 198712, coll. J. Carey, January 1978; same locality, habitat, date and collector, 4, USNM 97486; 4, BMNH ZB1985.82-85; 4, AHF 1435.

Size range of paratype specimens 20 setigers, 1.2 mm length, 0.6 mm width to 71 setigers, 7.6 mm length, 0.9 mm width.

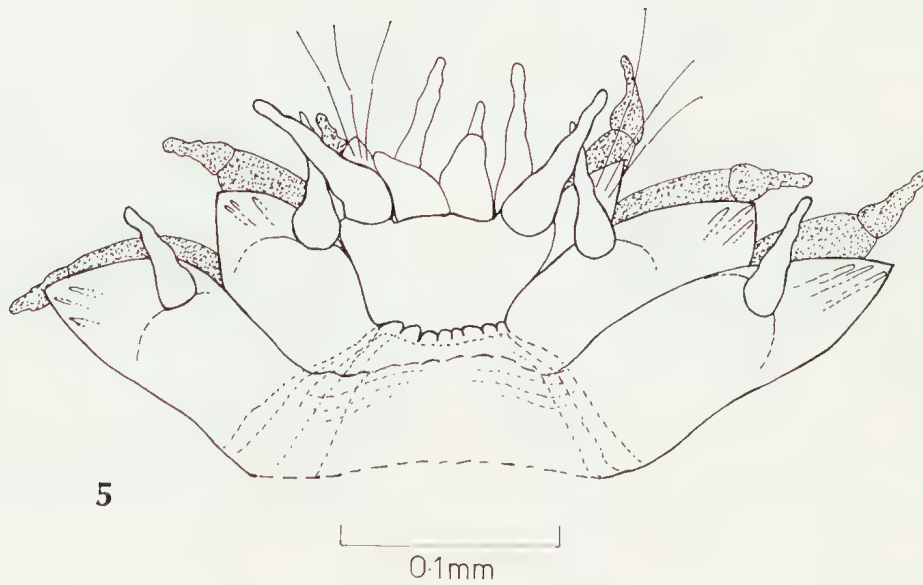
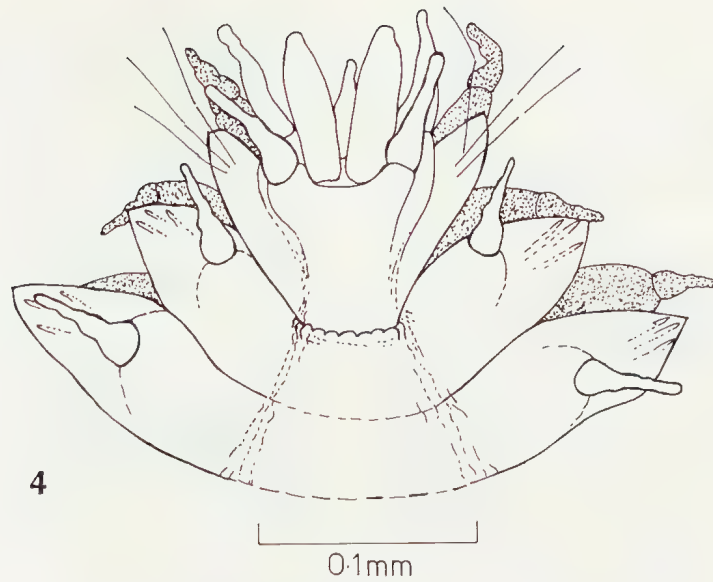
Additional material. Australia, Queensland, Halifax Bay, Stn F (19°10'S, 146°38'E), slightly gravelly, muddy sand, 5 m, 4, NTM W. 1681, coll. J. Carey, July 1977; Stn F, 5 m, 8, NTM W.1686, coll. J. Carey, February 1980; Stn C (19°10'S, 146°37'E), muddy sand, 2 m, 9, NTM W.2053, coll. J. Carey, January 1978; Stn A (19°07'S, 146°33'E), muddy sand, 2 m, 20, NTM W.1684, coll. J. Carey, February 1979; Stn A, 12, NTM W.1685, coll. J. Carey, January 1980; Brisbane River, Quarantine Station, Stn 2, 1, AM W.7466, coll. D.F. Boesch, 1972; Moreton Bay, Bramble Bay, 80–90% sand and mud, 5.4 m, 1, QM GH 10622, coll. S. Cook, 12 December 1972; Bramble Bay, Stn 3B, shell grit and mud, 1, QM GH613, coll. I.P., April 1975; Stn 3B, shell grit and mud, 1, QM GH614, coll. I.P., June 1975; Stn 3C, shell grit and mud, 5.4 m, 1, QM GH612, coll. I.P., April 1975; Northern Territory, Gove, Mangrove Creek, Stn 4B, mud and sand, intertidal, 1, NTM W.1676, coll. N.T. Fisheries, 22 June 1971; Stn 3, mud, intertidal 1, NTM W.1675, coll. N.T. Fisheries, 14 December 1970. Papua New Guinea, Port Moresby Harbour, Tatana Island, Stn 1, fine calcareous mud at base of reef, 20–25 m, 7, NTM W.1678, coll. J. Watson, June 1981; Stn 2, same locality and habitat, 8, NTM W.1679, coll. J. Watson, June 1981; Vahunabada Reef, Stn 3, same habitat, 2, NTM W.1677, coll. J. Watson, June 1981; Esade Reef, Stn 4, same habitat, 2, NTM W.1680, coll. J. Watson, June 1981.

Description. Holotype with anterior segments retracted (Fig. 6). Tips of prostomial and peristomial appendages visible above nuchal fold. Two pairs of red eyes faintly visible beneath nuchal fold. Notosetae comprising: 3–8 lateral paleae with 3–5 ribs (Fig. 8); 2–3 slender paleae with 9–15 ribs inserted between lateral and main groups; 15–17 main paleae with 17–22 (24 maximum) ribs and 3–6 raised and finely serrated ribs; 2–3 median paleae with 9–22 ribs and 0–3 raised ribs consisting of 2 distal median paleae with 13–22 ribs plus a smaller, slightly pointed proximal median with 9–12 ribs. One small, slender palea (½ length of main), with 8 ribs, and 0–2 raised ribs inserting between the main and median groups on posterior 10 setigers. Medium to small granules on superior surface of main and distal median paleae. Dorsal cirrostyle retractile within cirrophore (Fig. 7).

First and second neuropodia with neurosetae spinigers only. Subsequent neurosetae with superior group of 4 spinigers with long, slim shafts present from anterior setigers to mid-body setigers; 3 with long blades and fine basal dentition (Fig. 9a), and 1 with slightly shorter



Figs 2-3. *P. setula*, anterior end, dorsal view (above) and ventral view (below). *m.a.*, median antenna; *la.*, lateral antennae; *p.*, palp; *dt.c.*, dorsal tentacular cirrus; *vt.c.*, ventral tentacular cirrus; *dc.set. I.*, dorsal cirrus setiger 1; *dc.set. II.*, dorsal cirrus setiger 2; *vc.set. II.*, ventral cirrus setiger 2; *n.f.*, nuchal fold; *m.f.*, mouth flap; *p.i.*, paleae insertion (Paratype NTM W.1674).



Figs 4-6. *P. setula*: 4, anterior end, ventral view, relaxed (Paratype NTM W.1674); 5, anterior end, ventral view, half retracted (NTM W.2053); 6, anterior end, ventral view, retracted (Holotype NTM W.1673).

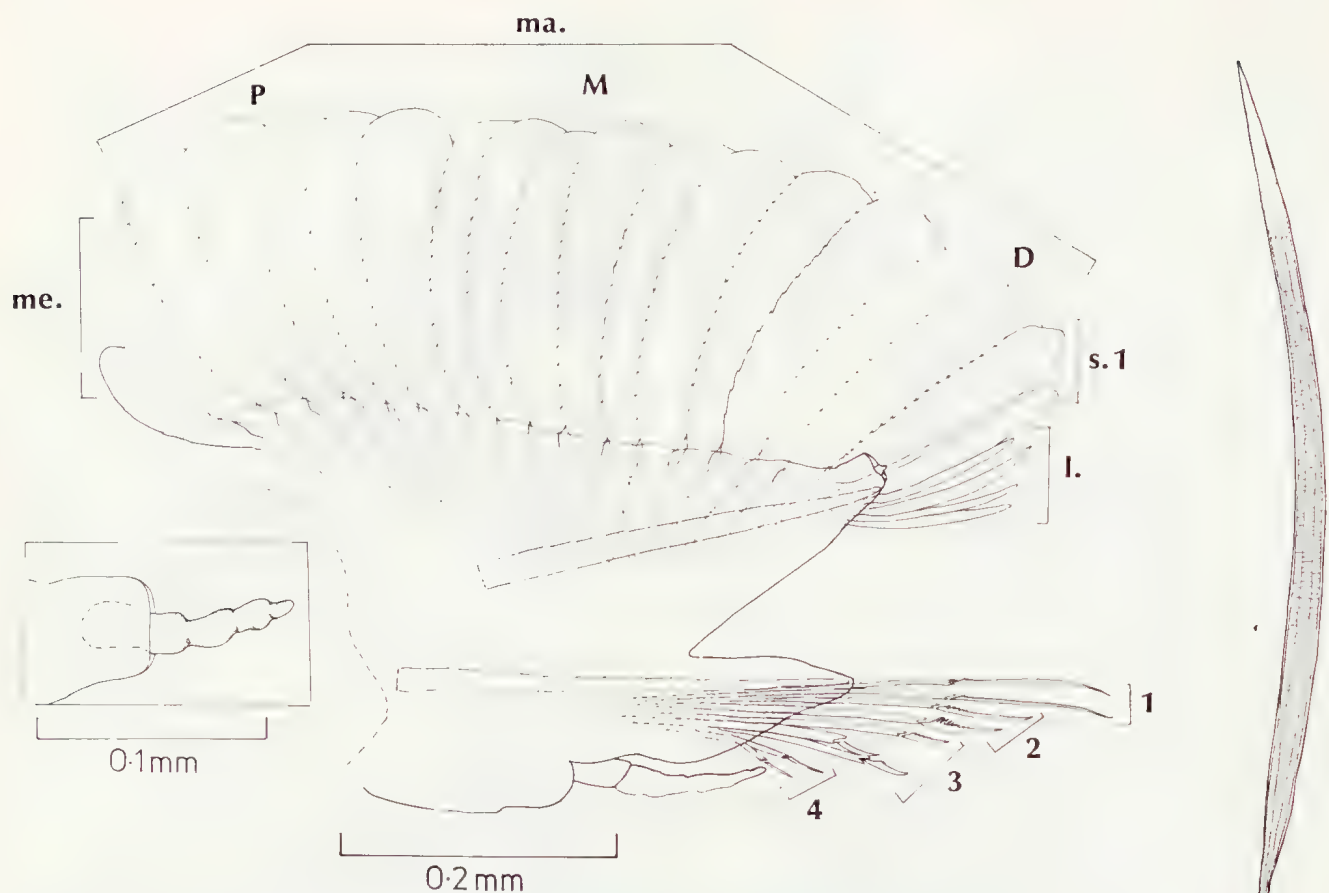


Fig. 7. *P. setula*, setiger 30, ventral view. Notosetal units: **l.**, lateral; **s. 1**, subunit 1; **ma.**, main; **D**, distal; **M**, mid; **P**, proximal; **me.**, median. Neurosetal units: **1**, superior spinigers; **2**, mid-superior falcigers; **3**, mid-inferior falcigers; **4**, inferior spinigers; **inset**: dorsal cirrus, relaxed (Holotype NTM W.1673).

0.04 mm

Fig. 8. *P. setula*, lateral palea (Holotype NTM W.1673).

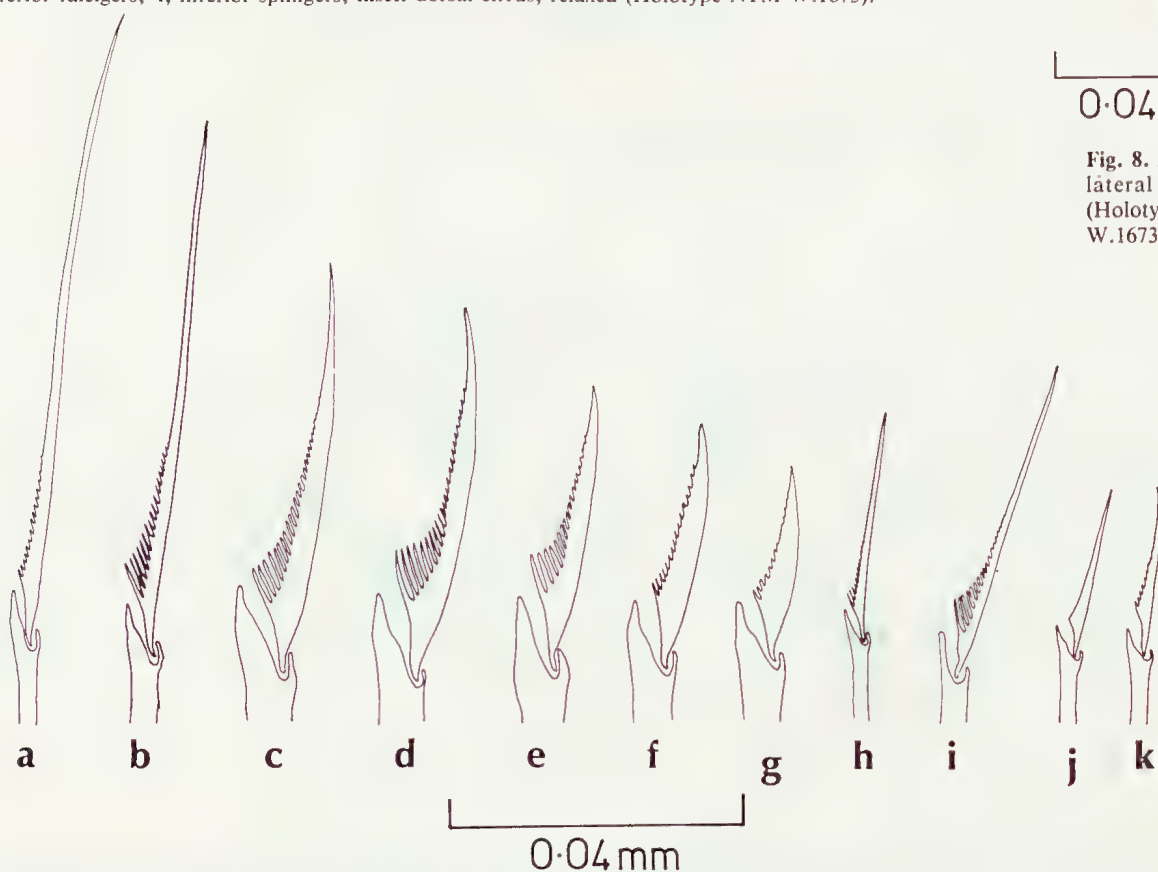


Fig. 9. *P. setula*, setiger 34, neurosetal units: **a-j**, Holotype NTM W.1673; **k**, NTM W.1686.

blade and more pronounced basal dentition (Fig. 9b). Up to 3 superior spinigers, including 1 with short, fine blade (Fig. 9i), present in posterior setigers. Mid-superior group with 6–8 falcigers with medium length blades each with coarse basal dentition (Fig. 9c, d). Mid-inferior group with 6–10 falcigers with short blades and finer basal dentition (Fig. 9e, f, g). Inferior group of 4–5 spinigers with slim, short shafts and narrow blades with very fine basal dentition (Fig. 9h). Pygidium quadrate with 2 anal cirri located on lateral posterior edge (Fig. 12).

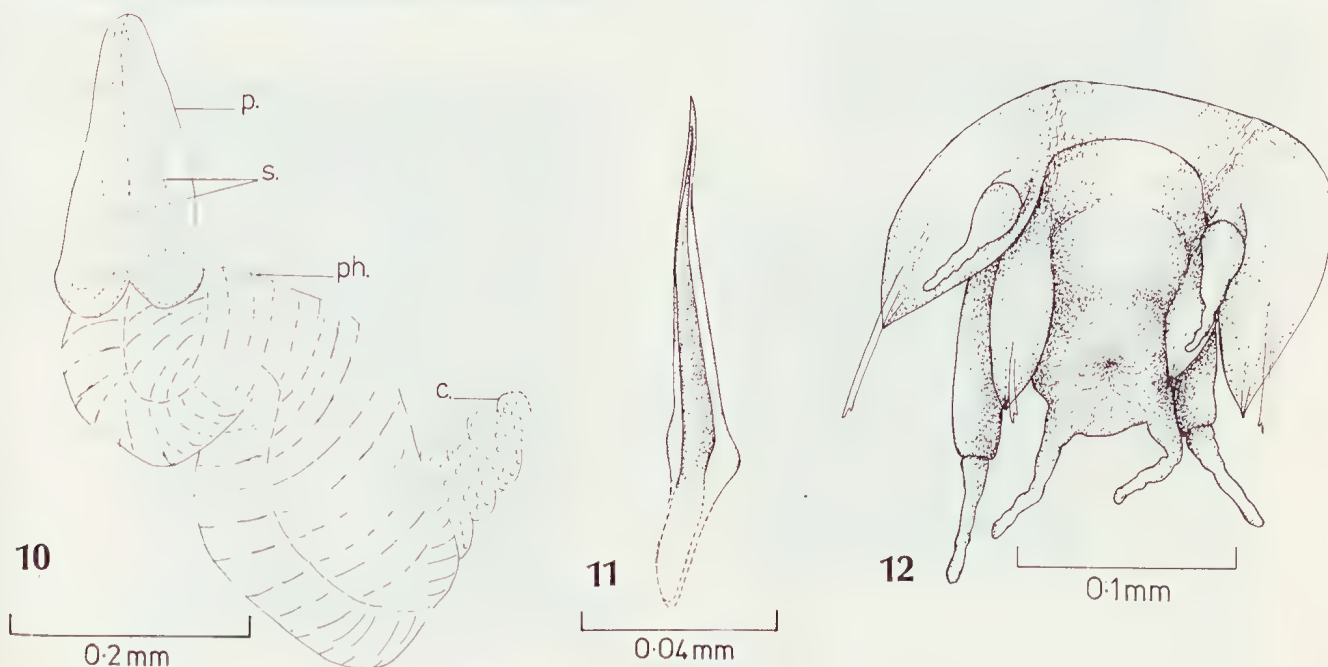
ADDITIONAL MORPHOLOGICAL INFORMATION. Based on paratypes and other material.

Prostomium and three anterior segments. The prostomium in *Paleaequor setula* is small and compressed in between the anterior three segments. When these segments are relaxed, the prostomium and its appendages are clearly visible with the posterior pairs of eyes just posteriorly covered by the nuchal fold. (Paratype NTM W.1674, Fig. 2). The anterior three segments (peristomium, setiger 1 and 2) in conjunction with the prostomium (with which they are fused) are capable of retracting. At the point of greatest retraction, the appendage tips are only visible dorsally above the nuchal fold and ventrally above the mouth fold (Fig. 6). Three stages, relaxed, semi-retracted and retracted, based on *P. setula* specimens but characteristic for all *Paleaequor* species, are figured in ventral view (Figs 4,5,6). The degree of fusion is complex within the three segments. In Fig. 2 the peristomial segment dorsally appears separated from setiger 1, and in Fig. 3, ventrally it appears fused to setiger 1. In dorsal aspect, setigers 1 and 2 appear fused but ventrally there is a clear segmental line between setiger 1 and 2. Further study is needed to elucidate the retraction mechanism.

Stylets. A mouth flap, which appears as a horizontal wrinkled ridge (Fig. 3), opens on the anterior margin of setiger 2 (or segment 3). Sometimes the proboscis may be partly extruded through the mouth opening with the two tips of the stylets visible. When the proboscis is relaxed the stylets may be seen through the ventral body wall at a level between the 3rd and 5th setigerous segments.

Upon dissection, the pharynx is revealed as an elongate, strongly muscular organ which is characteristically bent midway (Fig. 10). Small caeca are present posteriorly. Anteriorly, a constriction separates the proboscis, which contains two stylets, from the remainder of the pharynx. In situ, ventrally, the two transparent stylets are set close, each with the groove facing one another. They are extremely fragile and difficult to excise entire. A longitudinal groove runs the entire length of the stylet, narrowing distally. The proximal third of the stylet widens and flares out laterally; it appears to be attached to the proboscis wall at this point. Proximally, the base of the stylet is extremely fragile so this section has not been dissected out entire and observed in detail (Fig. 11).

Variations in setal counts. *Paleaequor setula* shows some variation in setal counts between setigers and between individuals of different size. Table 1 shows, for an entire specimen of 81 setigers (NTM W.2053), differences between setigers in the numbers of paleae within the notosetal fascicle, the number of ribs on the various paleae types and the numbers of different neurosetal types. There is a decrease in the number of lateral, main and median paleae within the anterior and posterior 10 setigers. The larger number of ribs on the main paleae is concentrated in the mid group and occurs on the mid-body setigers. Main paleae with a higher



Figs 10–12. *P. setula*: 10, pharynx and proboscis, ventral view (s., stylets in situ; p., proboscis; ph., pharynx; c., caeca); 11, stylet, ventral view (NTM W.2053); 12, pygidium, ventral view (Holotype NTM W.1673).

Table 1. Comparison of setal counts between setigers of an 81 setiger individual of *P. setula* NTM W.2053

Setiger number	1	2	4	5	11	13	28	42	51	74	77	79	81
Notosetal characteristics													
Lateral paleae (number)	1	2-3	4	4	4	5-6	4	4	4	3	3	2	1
Number of ribs	3-5	3-5	2	2	2-3	2-3	2-3	2	2-3	2	4	3	3
Lateral, sub-unit 1 (number)	0	0	2	2	3	3	3	3	2	2	2	2	2
Number of ribs	0	0	*	*	11,12,15	11,12,15	10,12,15	*	9,13	12,12	9,13	13,14	11,14
Main paleae (number)	2	4	8-9	11	14-15	14-15	14-15	16	16-17	12-13	10	6	3
Number of ribs (distal)	8	14	17	18	21	21	20	20	20	19	16	17	17
Number of ribs (mid)	0	15-16	18	20	21-23	21	21	23	21-24	20-21	20-21	18-22	18
Number of ribs (proximal)	0	14	17	18	*	*	20	21	22	19	19	21	20
Median paleae (number)	0	1	1	*	2	2	2	2	2	2	2	3	1
Number of ribs (distal)	0	12	18	*	*	*	20	21	20	19	20	20	20
Number of ribs (proximal)	0	0	0	*	*	*	17	18	*	15	*	12,18	0
Presence (+), absence (-) of single palea, sub-unit 2	-	-	-	-	-	-	-	-	-	+	+	+	+
Neurosetal characteristics													
Superior spinigers (number)	9	10	3-4	4	4	4	4	4	4	3	3	3	blades
Mid-superior falcigers (number)	0	0	6	6	6	7	7	7	6	6	5	4	all broken
Mid-inferior falcigers (number)	0	0	6	6	7	10	10	10	8	6	4	4	6 shafts
Inferior spinigers (number)	0	0	4-5	4-5	5	5	5	5	5	5	4	3	present

0 absent

* damaged or obscured

number of ribs (e.g. 23-24) are not consistently dispersed from setiger to setiger but appear only irregularly. The most proximal median paleae consistently possess a lower number of ribs compared to the most distal median paleae. The single palea (subunit 2) is only present in setigers 74 to 81. There is a slight decrease in numbers of neurosetal types in the anterior- and posterior-most setigers (with the exception of superior spinigers on 1st and 2nd neuropodia). The most noticeable change is the decrease of mid-inferior falcigers within the anterior and posterior 10 setigers.

Table 2 compares setal counts between six *P. setula* individuals of different size, ranging from 16 to 105 setigers. Setal counts also vary between individuals of different size. The numbers of main paleae and, to a lesser extent, lateral paleae increase with setiger size. The numbers of median paleae remain constant. Larger individuals also possess main paleae with a larger number of ribs. It should be noted, however, that these higher numbers of ribs of main paleae are not consistent from setiger to setiger within the individual (see example

Table 1). The higher numbers of lateral paleae of larger individuals also vary from setiger to setiger. For example, a specimen of 68 setigers, (NTM W.1673) with 4-6 lateral paleae on most setigers, has a single count of 8 on the 33rd notopodium; a specimen of 79 setigers (NTM W.1679), with 4-5 lateral paleae on most setigers, has 7 lateral paleae on 7 mid-body setigers.

Overall numbers of neurosetae (not included in Table 2) also increase with size. A specimen of 16 setigers (NTM W.1686) possesses a fascicle of 17; a specimen of 105 setigers (NTM W.1676) has 25-30 neurosetae per neuropodium on the mid-body setigers. There are small differences of neurosetal shape between individuals of different size, e.g. a specimen of 16 setigers (NTM W.1686) possesses smaller inferior spinigerous neurosetae (Fig. 9j) including some that could be described as falcigerous (Fig. 9k).

Occurrence with other genera. *Chrysopetalum* sp. (2) and a new chrysopetalid genus and species (8) (n. gen. 1, author ms. in prep.) were present with *P. setula* in samples from Stn A and G, Halifax Bay, Queensland.

Table 2. Comparison of setal counts with increasing number of setigers for 6 specimens of *P. setula*

Registration number	NTM W.1686	NTM W.1684	NTM W.1678	NTM W.1673	QM GH 10622	NTM W.1676
Locality	Halifax Bay, Queensland	Halifax Bay, Queensland	Port Moresby, Papua-New Guinea	Halifax Bay, Queensland	Moreton Bay, Queensland	Gove, Northern Territory
Setigers (number)	16	26	46	68	82	105
Length (mm)	1.2	2	3.7	9.2	14	12.6
Width (mm)	0.6	0.6	1.0	1.2	1.4	1.5
Lateral paleae (number)	2-3	3	3-4	4-6(8)	4-6(7)	4-6(7)
Main paleae (number)	7-9	12	12-14	15-17	18-20	18-20
Main paleae (number of ribs)	16-18	16-18	16-21	17-22(24)	17-22(24)	17-22(23)
Median paleae (number)	2-3	2-3	2-3	2-3	2	2

Note: all paleae counts based on mid-body setigers

Habitat. Type material was made available from samples from a nickel mining monitoring study carried out in Halifax Bay, Queensland (Carey, 1981). Inshore stations (B,C,D) are situated at tidal creek entrances with generally muddy sediments (grain size number in this habitat varies seasonally). Near-shore stations (A,E,F) have slightly gravelly, muddy sand as does the one offshore station (G). Stations A and G are situated near coral reefs (J. Carey, pers. comm.). Other material comes from sediments that range from shell grit and mud (Moreton Bay, Queensland: Stephenson, 1976) to calcareous muds at the bases of reefs (Port Moresby Harbour, Papua New Guinea: J. Watson, pers. comm.). Depth ranges from the intertidal to 25 m.

Distribution. Southern Queensland, Australia to Southern Papua New Guinea.

Etymology. The specific name, *setula*, is derived from the Latin diminutive meaning little bristle, in reference to the small inferior spinigerous neurosetae.

Paleaequor breve (Gallardo) new combination

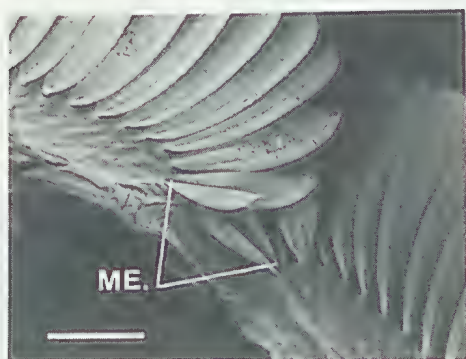
Figs 13–17

Bhawania brevis Gallardo, 1968: 54–55, pl. IX, figs 1–9, (Nha Trang, Vietnam).—Shin, 1980: 162–163.

Material examined. HOLOTYPE: Vietnam, Bay of Nha Trang, Stn 270 (12°15'N, 109°10'E), sandy mud, 22 m, AHF N.11593, coll. Gallardo, 23 March 1960; 127 setigers, 18 mm length, 1.3 mm mid-body width, 0.8 mm width anterior end, 0.6 mm width posterior end, specimen entire.

Additional material examined. Bay of Nha Trang, Stn 130, mud, 16m, 1, AHF N.11597, coll. Gallardo, 11 February 1960; Stn 74, sandy mud, 10 m, 2, AHF N.11596, coll. Gallardo, 20 January 1960.

Description. Holotype with anterior segments retracted. Tips of prostomial and peristomial appendages visible above nuchal fold. Two pairs of eyes, faintly visible beneath nuchal fold. Notosetae comprising: 3–4 lateral paleae with 3–4 ribs (Fig. 15); 2 slender paleae with 10–13 ribs inserted between lateral and main groups (Fig. 15); up to 17 main paleae with 16–20 ribs and 3–5 raised and very finely serrated ribs; 2–3 median paleae with 8–20 ribs and 0–3 raised ribs



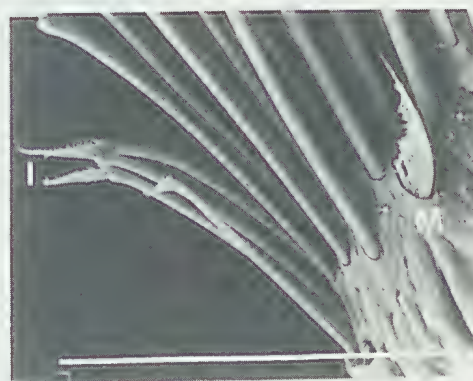
13



14



15



16

Figs 13–16. *P. breve*, setiger 65: 13, main and median (ME.) paleae (Holotype AHF N.11593); 14, median paleae, detail (Holotype AHF N.11593); 15, lateral (L) and subunit 1 (S.1) paleae (Holotype AHF N.11593); 16, lower part neuropodium (I, inferior spinigers; M, mid-superior falciger coming through neuropodium) (Holotype AHF N.11593). Scale lines = 100 μ m.

(Figs 13, 14), comprising 2 distal median paleae with 16–20 ribs, and a smaller, more pointed proximal median palea with 8–16 ribs. One small, slender palea ($\frac{1}{2}$ – $\frac{2}{3}$ length of main) with 8 ribs inserting between main and median groups on the posterior 10 setigers. Patchy, very fine granules on superior surface of main and distal median paleae.

Neurosetae comprising a superior group of 4 spinigers (Fig. 17a) on the anterior to mid-body setigers. Up to 3 spinigers present on each of the posterior setigers including 1 with short, fine blade (Fig. 17h). Mid-superior group has 6–8 falcigers with long to medium length blades with a coarse basal serration (Fig. 17b,c). Mid-inferior group has up to 9 falcigers with short blades and fine basal serration (Fig. 17d,e). Inferior group with 4–7 spinigers with slim, short shafts and attenuated blades with fine, long basal serration (Figs 16, 17f,g). Pygidium quadrate with 2 anal cirri located on lateral posterior edge.

Comments. Gallardo's (1968) diagrammatic figures of the retracted prostomium and three anterior segments of *Bhawania brevis* agree well with the anterior end described in this paper for *Paleaequor*. He stated that the eyes were absent. On inspection of specimens, two

pairs of eyes in fact are present, although their pigmentation is very faint and they are covered entirely by the nuchal fold. Shin (1980) observed two pairs of red eyes in specimens of this species (as *B. brevis*) collected off Hong Kong Island.

Gallardo recognized 'thin, blunt-tipped setae' and 'long paleae', which correspond here to the categories of lateral and main paleae. His description did not include the raised and serrated ribs of the main paleae which, in this species, are particularly shallow and very finely sculptured. Gallardo described four types and positions of neurosetae—'superior most ... spinigers,' 'lower and next lower ... falcigers' and 'lower most ... spinigers'. These descriptions agree closely with the neurosetal terminology proposed here. However, Gallardo's division of the neurosetal fascicle into supra and sub-acicula is incorrect, as all neurosetae insert below the ventral aciculum.

Habitat. Mud and sand sediments in depths of 10–22 m. From Hong Kong, Shin (1980) records 2 specimens from Kap Shui Mun in sandy mud (22 m) and 2 specimens from off Lamma Island in soft mud (26 m). Specimens were not examined by the author.

Distribution. South Vietnam; Hong Kong.

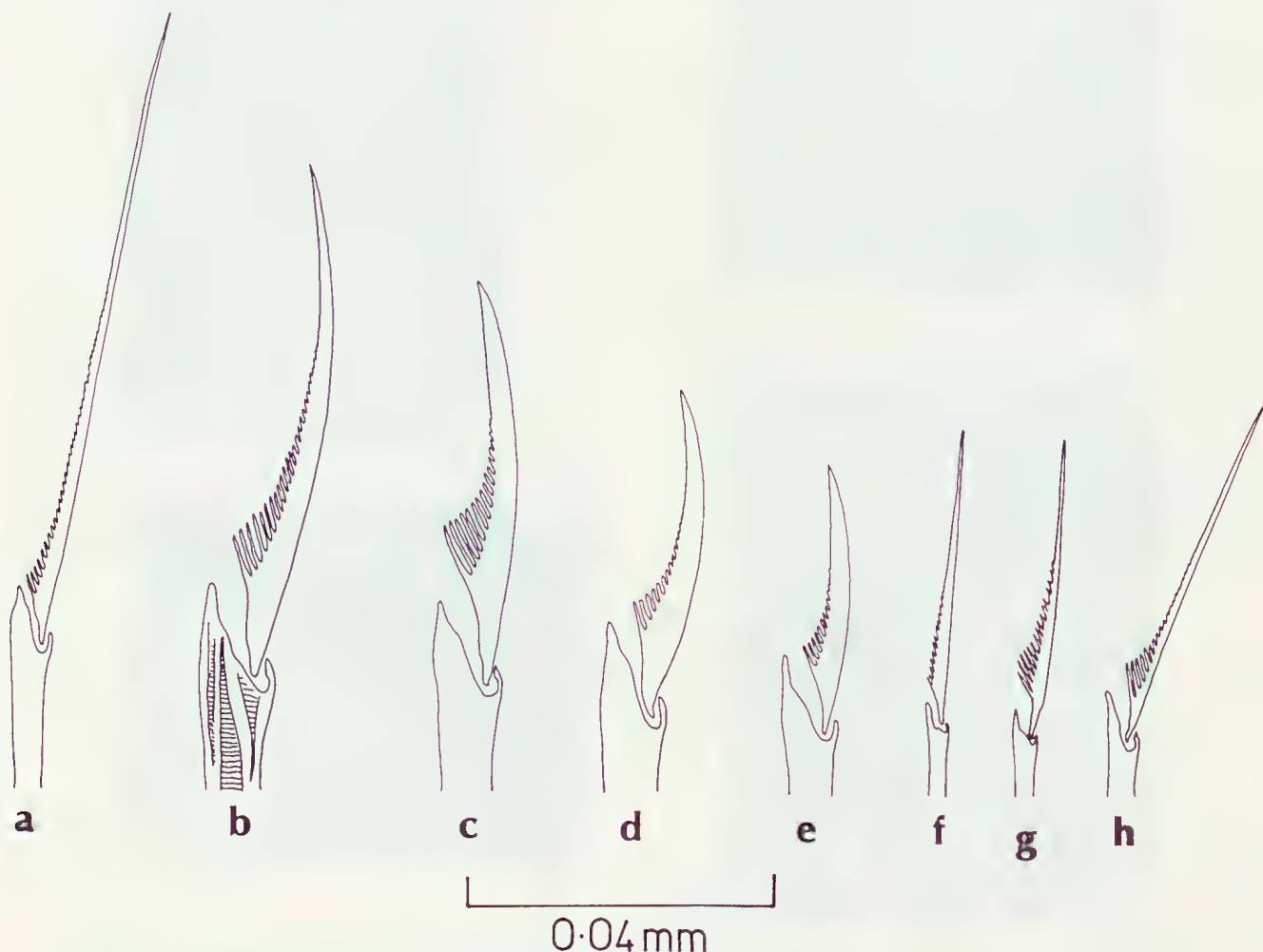


Fig. 17a–h. *P. brevis*, setiger 20, neurosetal units (Holotype AHF N.11593).

Paleaequor heteroseta (Hartman), new combination
Figs 18–21

Paleanotus heteroseta Hartman, 1945: 12, pl. 1, figs 1–6, (North Carolina, U.S.A.).—Renaud, 1956: 9, fig. 5; Day, 1973: 14; Wilson, 1979: 627; Gardiner, 1982: 100, fig. 5f–i; Gathof, 1984: 26–29, fig. 8a–g.

Material examined. HOLOTYPE: United States, North Carolina, Beaufort, Bogue Sound, No. 0090 (originally No. 70), dredged shell fragments, 'shallow depths', 15 June 1940, AHF N.1545; 62 setigers, 7 mm length, 0.84 mm width, specimen entire.

Additional material examined. Virginia, York River, 1, USNM 56559, coll. G.R. Gaston, March 1976. North Carolina, off Beaufort, sand and broken shell, 10 m, 53, USNM 51005, coll. J.H. Day, 19 April 1965; Cape Lookout, among *Petaloproctus socialis* colonies, intertidal, 10, USNM 52859, coll. S. Gardiner, 17 August 1974; same locality and habitat, 30, USNM 52860, coll. H. Wilson, November 1974. Florida, Indian River, 1, MNHN A870, coll. J.L.T., 8 July 1963; St. Lucie Co., Hutchinson Island, (27°22'08"N, 80°13'46"W), 11.5 m, 1, USNM 54227, coll. Gallagher et al., 1 March 1972; same locality; 10.9 m, 1, USNM 54226, coll. Gallagher et al., 5 March 1973. Gulf of Mexico, Florida, Panama City, offshore, (30°03'06"N, 86°08'08"W), 24, USNM 97885, 8 April 1958; Panama City, 12 mi. offshore, 30 m, 20, USNM 97856, coll. M.L. Jones et al., 9 September 1959; Tampa Bay, 100, USNM 45522, coll. John L. Taylor, 29 October 1963; Gulf of Mexico, 29°20'04"N, 84°44'03"W), Stn 2423, 30 m, 39, USNM 55803, coll. R/V *Columbus Iselin*, July 1976. Texas, off Freeport, 18 m, 2, USNM 51471, coll.

D.E. Harper; Port Aransas, 6, USNM 97857, coll. M.L. Jones, dredge, June 1962; Lydia Ann Channel, associated with chaetopterid tube, 3, USNM 97860, coll. M.L. Jones, 2 July 1962; same locality and collector, off abandoned lighthouse, 1, USNM 97858, 19 June 1962; same locality and collector, between beacon 83 and buoy N84, 2, USNM 97859, 19 June 1962.

Description. Holotype with anterior segments retracted in part. Prostomial and peristomial appendages visible dorsally above nuchal fold. Two pairs of red-brown eyes visible; anterior pair above nuchal fold and posterior pair beneath nuchal fold.

Notosetae comprising 3–4 lateral paleae with 5–9 ribs (Fig. 19 left); 2 slender paleae with 10–15 ribs inserting between lateral and main groups; up to 14 main paleae with 17–22 (24 maximum) ribs and 3–6 raised and finely serrated ribs (Fig. 18a,b); 3–4 median paleae with 11–25 ribs and 0–5 raised ribs, comprising 2 broad, distal paleae with 20–25 ribs, the next proximal palea smaller with 17–21 ribs and the most proximal and smallest with 11–17 ribs. One small, slender palea ($\frac{1}{2}$ to $\frac{2}{3}$ the length of main palea) with 10–13 ribs and 2–3 raised ribs inserting between the main and median groups of paleae on the setigers of the posterior half of the body. Large to medium granules on superior surface of main and distal median paleae.

Neuropodium long and pointed. First and second neuropodia with neurosetae composed of spinigers only

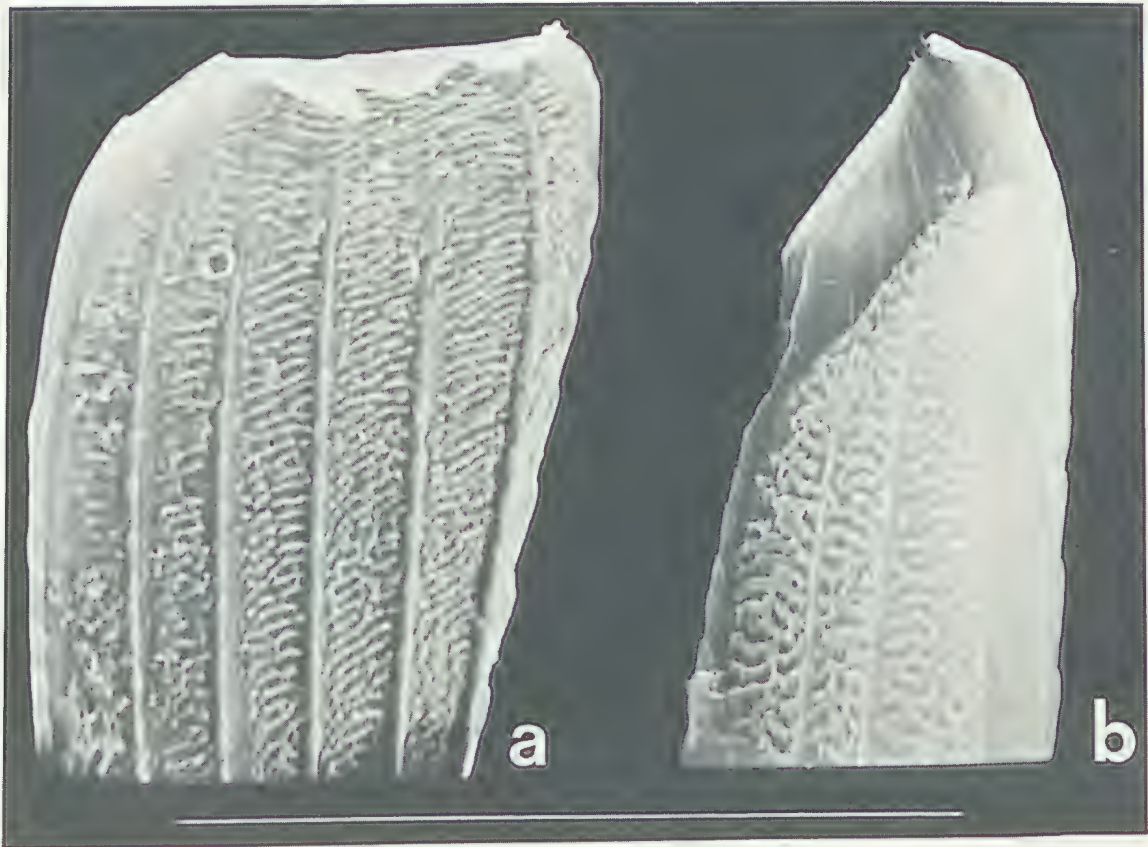


Fig 18. *P. heteroseta*, setiger 31, main paleae, distal third; scale line 100 μ m (a, mid main palea; b, distal main palea) (Holotype AHF N.1545).



Fig. 19. *P. heteroseta*: left, setiger 30, lateral palea (Holotype AHF N.1545); right, setiger 5 of juvenile, dorsal view (USNM 97856).

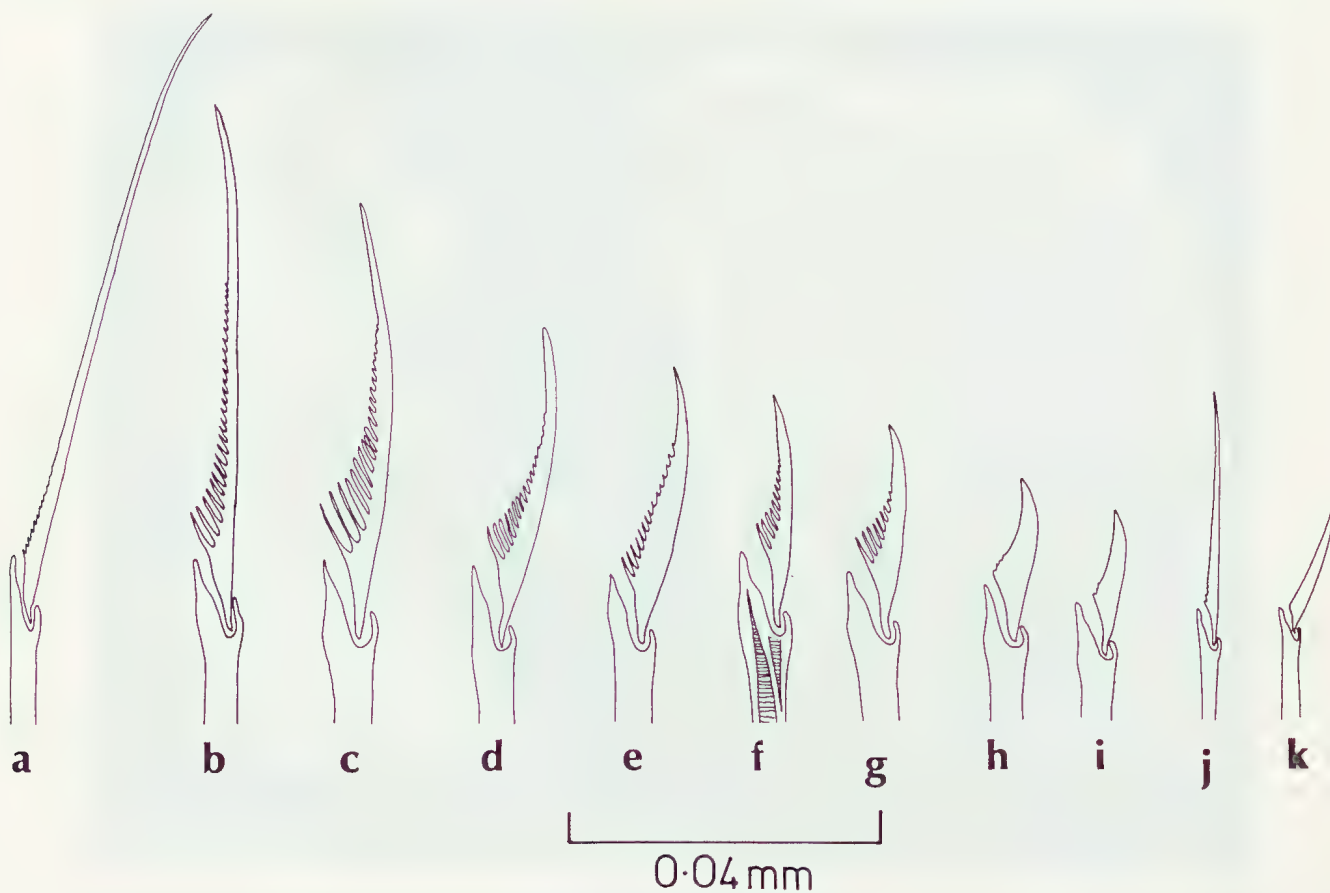


Fig. 20a-k. *P. heteroseta*, setiger 30, neurosetal units (Holotype AHF N.1545).

of which up to 4 may persist to setiger 10. Subsequent neurosetae with superior group of 2 spinigers with long, slender shafts and long blades (Fig. 20a) on each setiger from anterior to mid-body region. Posterior setigers with up to 3 spinigers, including 1 with a short, fine blade (Fig. 20j). Mid-superior group with up to 7 falcigers, including 1–2 with long blades (Fig. 20b) and others with medium length blades with coarse basal serration (Fig. 20c,d). Mid-inferior group with 8–12 falcigers with medium to short blades with coarse to fine basal serration (Fig. 20e,f,g). Inferior group with up to 6 falcigers with slender, short shafts and short blades with fine basal serration (Fig. 20h,i). A single falciger with a narrow blade is found within the inferior group of neurosetae in the posterior 10 setigers (Fig. 20k). Pygidium composed of rounded dorsal structure with 2 short anal cirri and a small ventral cone (Fig. 21).

ADDITIONAL MORPHOLOGICAL INFORMATION

Variation in setal counts. *Paleaequor heteroseta* shows some variation in setal counts between setigers and between individuals of different size. Table 3 shows, for an entire specimen of 61 setigers (USNM 51005), differences between setigers in the numbers of paleae within the notopodium; the numbers of ribs on the various paleae types; and the numbers of different neurosetal types. There is a decrease in the numbers of main paleae in the anterior and posterior 10 setigers. The larger number of ribs on the main paleae are concentrated in the mid group of the main paleae fan and occur on the mid-body setigers. Main paleae with a higher number of ribs (e.g. 23, 24) are not consistently dispersed from one setiger to the next and appear irregularly. The large distal median paleae possess a consistently high number of ribs from the 10 setiger onwards, compared to the smaller proximal median

paleae. The single paleae (subunit 2) is present in setigers 26 to 61. There is a slight decrease in numbers of neurosetal types in the anterior- and posterior-most setigers (with the exception of the superior spinigers in the anterior four setigers).

Setal counts also vary between individuals of different size. For example, a specimen of 9 setigers (USNM 97856) has a fan of 5 main paleae, whereas the type specimen of 62 setigers (AHF N.1545) has a fan of 14 main paleae. The numbers of ribs of the main and median paleae increase with setiger size. The numbers of mid-inferior falcigers increase with setiger size. Specimens of 72 setigers (USNM 45522) and 61 setigers (USNM 51005) possess 10–12, whereas a specimen of 32 setigers (USNM 45522) has 6–8 and a specimen of 9 setigers (USNM 97856) has 5–8.

Notes on *P. heteroseta* juveniles. Specimens of 9 and 13 setigers (USNM 97856) have an ovoid body shape and a more convex dorsum in comparison to the long, narrow body shape and the very slightly convex to flattened dorsum of the adult. The two juveniles also possess silvery, almost transparent paleae in contrast to the usual golden brown paleae of the adult.

The 9 setiger individual has 0–1 lateral palea with 4–6 ribs. All notopodia have a tiny simple seta located just posteriorly to, or overlying the dorsal aciculum. Two slender paleae (subunit 1) with 12 and 13 ribs insert in between the lateral and main groups. There are up to 5 main paleae on each setiger with 15–18 ribs and 0–5 raised ribs. The three median paleae have 14–21 ribs (Fig. 19 right). Neurosetae resemble the four categories found in the adult and neurosetae numbers are as follows: superior 2, mid-superior 4, mid-inferior 5–8, and inferior 3–4.

Comments. In her description of *Paleanotus* (= *Paleaequor*) *heteroseta*, Hartman (1945) recognised two types of neurosetae and their three positions within the fascicle which correspond to the superior, mid and inferior positions designated by the author. Approximate numbers of neurosetae within each category given by Hartman agree with the numbers cited here. The 'narrower' and 'broader' paleae designated by Hartman correspond to the author's categories of lateral and main paleae. Her description did not include the raised and serrated ribs of the main paleae.

Other chrysopetalids incorrectly referred to *P. heteroseta*. Mileikovsky (1962) described some chrysopetalid larvae collected from the Gulf Stream (37°35' N, 70°48' E) as *Paleanotus heteroseta*. These specimens of 4 and 5 setigers possess symmetrical main paleae with longitudinal ribs, horizontal striae and strongly serrate margins that all extend to the apex of the palea. The 9 setiger specimen of *P. heteroseta*, described above, has main paleae with finely serrated margins and distinct hyaline tips that closely resemble those of the adult. As Mileikovsky's specimens are lost (R. Levenstein, pers. comm.) it is difficult to determine to what chrysopetalid genus these larvae belong.

Specimens of *Paleanotus* (= *Paleaequor*) *heteroseta*

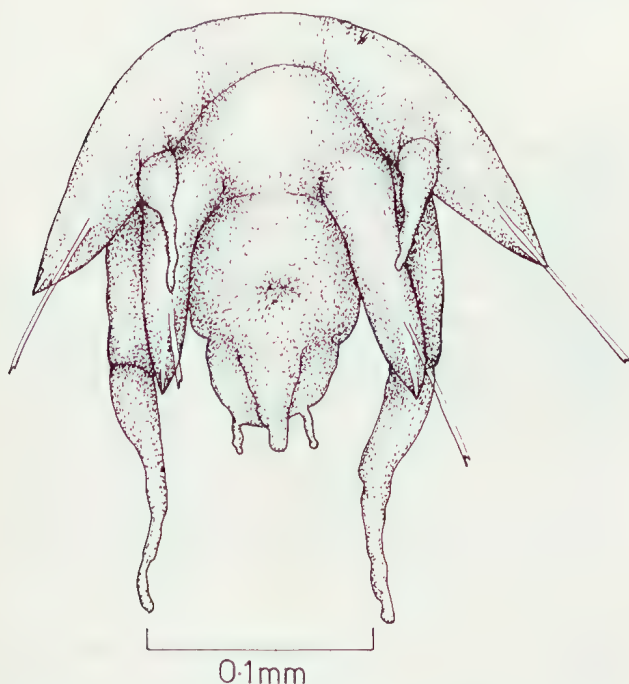


Fig. 21. *P. heteroseta*, pygidium, ventral view (USNM 52859).

Table 3. Comparisons of setal counts between setigers of a 61 setiger individual of *P. heteroseta* USNM 51005

Setiger number	1	2	4	6	10	18	26	36	48	51	55	58	60
Notosetal characteristics													
Lateral paleae (number)	1	2	3	4	3-4	3-4	3	3	3	2	2	3	1
Number of ribs	5	5	4-7	4-8	4-8	6-8	6-7	6	4-7	4-6	6-7	6-7	6
Lateral, sub-unit 1 (number)	0	0	1	1	1	1	2	2	2	2	2	2	2
Number of ribs	0	0	15	*	15	15	13,13	13,14	15,15	13,14	13,14	12,15	13,13
Main paleae (number)	3	7	8	10	11	10	13	12	10	9	7-8	6	2
Number of ribs (distal)	10	16	18	*	17	19	17	18	18	19	19	18	17
Number of ribs (mid)	0	18	19	*	20	21-23	21-23	22-24	23	21-24	22	21	18
Number of ribs (proximal)	0	17	20	*	20	22	22	21	20	20-22	23	22	0
Median paleae (number)	0	2	2	3	3	4	3	4	4	4	4	4	3
Number of ribs (distal)	0	18	*	18,18	21,21	24,20	24,20	23,22	25,20	25,23	24,23	23,20	23
Number of ribs (proximal)	0	17	*	17	19	**	19	19,16	**	20,17	20,16	17,11	18,13
Presence (+), absence (-) of single palea, sub-unit 2	-	-	-	-	-	-	+	+	+	+	+	+	+
Neurosetal characteristics													
Superior spinigers (number)	10	5-7	4	2	2	2	2	2	2	3	3	2	2
Mid-superior falcigers (number)	0	4-5	6	7	5	6	6	5	5	5	4	3	1
Mid-inferior falcigers (number)	0	0	3	12	10	10	8	10	12	10	6	*	2
Inferior falcigers (number)	0	0	3	4	4	4	4	4	4-5	4-5	5	5	2

0 absent

* damaged or obscured

were reported from the Cape Verde Islands by Rullier (1964). This material in the Paris Museum is misidentified. Rullier's specimens represent two species belonging to the genera *Paleanotus* and a new genus.

Occurrence with other genera. Collections from the Gulf of Mexico reveal *Chrysopetalum occidentale*, *Paleanotus chrysoplepis* and a new chrysopetalid genus and species (n. gen. 1) occurring within the same samples of *P. heteroseta* (Gathof, 1984). *Paleaequor heteroseta* has been collected in larger numbers (e.g. 100 specimens, USNM 45522) compared to the mostly single specimens of other chrysopetalid genera. In one lot (USNM 97856) a sample was composed of approximately half *P. heteroseta* and new genus 1, the majority of which were juveniles in both cases. *Bhawania goodei* has been recorded from the same general localities as *P. heteroseta* along the eastern United States coast but they never occur in the same sample. The two genera are found in different habitats; *Bhawania* being recorded from under rocks and in association with corals in shallow depths (both records Day, 1973; Gardiner, 1982), and *Paleaequor* from sandy and muddy sediments.

Habitat. *Paleaequor heteroseta* has been recorded from localities along the eastern seaboard from Northern Carolina (Hartman, 1945) to Indian River, Florida (Renaud, 1956). Recent collections by G. Gaston from York River, South Virginia represent a northward extension of range. The sites of these localities are largely composed of sheltered bays and submarine banks near entrances to rivers. Depth ranges from the intertidal to 12 m, and sediments are recorded as coarse sand, and sand and broken shell (Hartman, 1945; Day, 1973; Gardiner, 1982; Wilson, 1979). Wilson (1979) records *P. heteroseta* occurring as one of the numerically

dominant species in a polychaete community associated with maldanid sedimentary reefs on a sand flat at Point Lookout, North Carolina.

Localities in the Gulf of Mexico range from Tampa Bay, Florida to Port Aransas, Texas in depths to 30 m. Gathof (1984) records scattered occurrences of *P. heteroseta* for the northwest and northeast end of the Gulf of Mexico in sediments which range from sandy clayey silt and fine to coarse sand, in depths of 14-82 m.

Distribution. Eastern coast of United States to Gulf of Mexico.

Paleaequor psamathe n. sp.

Figs 22-24

Material examined. HOLOTYPE: Mexico, Gulf of California, Sonora, Pelican Point, (31°20'N, 113°38'W), USNM 97850, coll. B. Burch, 10 May 1969; 54 setigers, 3.6 mm length, 0.8 mm width, specimen entire. PARATYPES: Pelican Point, (31°20'N, 113°40'W), 13.6 m, 3, USNM 97851, coll. B. Burch, 30 September 1967.

Additional material examined. Gulf of California, Punta Cholla, intertidal, 7, AHF N.14112, coll. S.A. Glassell, 9 May 1941; off Cholla, 31°20'N, 113°41'W, rock and gorgonian bottom, 10.3 m, 6, CAS 17395, coll. T.A. Burch, 31 May 1968; Bahia Coastcomate, Jalisco, 60 km. NNW of Manzanillo, Colima and 3 mi. NW of Barra de Navidad, Stn RAD 1-68, under rocks and sand beneath rocks, 3-18 m, 1, USNM 97854, October 1968. Ecuador, Gulf of Guayaquil, Stn 773-D, (02°49'S, 80°31'W), 20 m, 2, USNM 97853, coll. Anton Bruun CR. 18B, 11 September 1966; Stn 773 (02°43'S, 80°33'W), 20 m, 8, USNM 97852, coll. Anton Bruun CR. 18B, 11 September 1966.

Range of specimens from Gulf of California and Western Mexico, 31 setigers, CAS 17395, 2 mm length, 0.45 mm width to 74 setigers USNM 97854, 8.7 mm length, 0.65 mm width.

Range of specimens from Gulf of Guayaquil, 13 setigers, 1.04 mm length, 0.5 mm width to 53 setigers, 4.4 mm length, 0.6 mm width; both USNM 97852.

Description. Holotype with prostomium and anterior segments retracted in part, two pairs of red-brown eyes visible dorsally. Notosetae comprising: 3–4 lateral paleae with 4–7 ribs; 2 slender paleae with 10–13 ribs inserted between lateral and main groups; up to 13 main paleae with a maximum of 21 ribs with 5–6 raised and finely serrated ribs; 4 median paleae with 13–25 ribs and 0–6 raised ribs, comprising 2 broad, distal paleae with 20–25 ribs, the next proximal palea smaller with 18–20 ribs, and the most proximal and smallest with 13–15 ribs. One slender palea ($\frac{2}{3}$ length of main palea) with 10–13 ribs and 2 raised ribs inserting between the main and median groups on the posterior half of the body (Fig. 22). Large, scattered to dense granules on superior surface of main and distal median paleae.

Neuropodium short and conical (Fig. 23). First setigerous neuropodium with neurosetae spinigers only, of which up to 4 persist to setiger 5. Subsequent neurosetae with superior group of 2 spinigers, with slim shafts and fine attenuated blades (Fig. 24a), present on each setiger to mid-body region. Posterior setigers each with up to 3 spinigers, including 1 with a short, hair like blade (Fig. 24i). Mid-superior group with 4–6 falcigers with medium length blades and coarse basal serration (Fig. 24c,d). Within this group a long-bladed falciger present only on the anterior segments (Fig. 24b). Mid-inferior group with 8–10 falcigers with medium to short blades (Fig. 24e,f,g). Inferior group of 3–5 falcigers with short shafts and short, broad blades with fine basal serration, and terminating in a blunt, smooth tip (Fig. 24h). Single falciger with a narrow blade included within inferior group on posterior 10 setigers (Fig. 24j). Pygidium rounded, dorsal structure with 2 short anal cirri and a ventral cone.

Comments. The specimen from near Barra de Navidad, western Mexico (USNM 97854) is long and slim with a white body and near transparent paleae. Neurosetae and paleae types are similar to those specimens from the Gulf of California. The neurosetae of the posterior segments are sparse and mostly broken.

Ecuadorian specimens of *P. psamathe* differ slightly from those of the Gulf of California. Characters that distinguish the Guayaquil population include a higher number of ribs in the main (up to 22) and median paleae (16–26). There appear to be no long falcigers present in the upper mid-superior group, and the lower mid-superior falcigers are slightly shorter with characteristic long basal serration on the blades.

At present, *P. psamathe* appears to have a disjunct distribution with a northern population extending from 31° to 19°N and a southern population recorded from 2°S (Fig. 1).

Occurrence with other genera. One specimen of *Paleanotus* sp. was found in one sample with *P. psamathe* (USNM 97851). *Paleanotus* sp. and

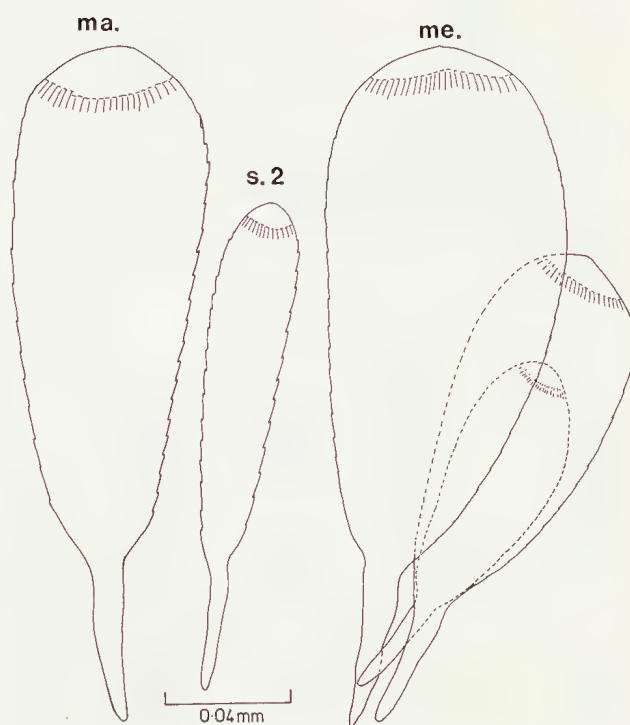


Fig. 22. *P. psamathe*, setiger 33; **ma.**, proximal main palea; **s.2**, subunit 2 palea; **me.**, median palea (Holotype USNM 97850).

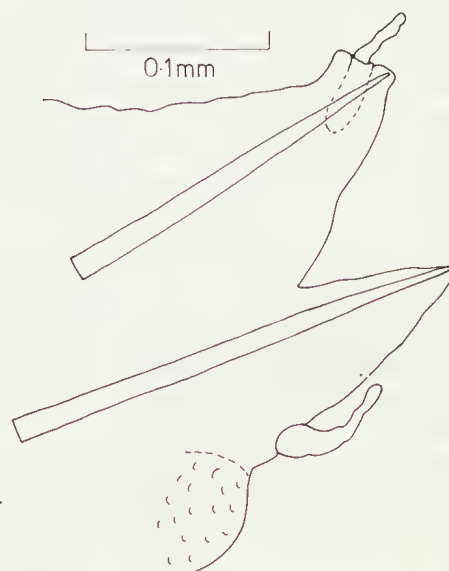


Fig. 23. *P. psamathe*, setiger 34, ventral view (Holotype USNM 97850).

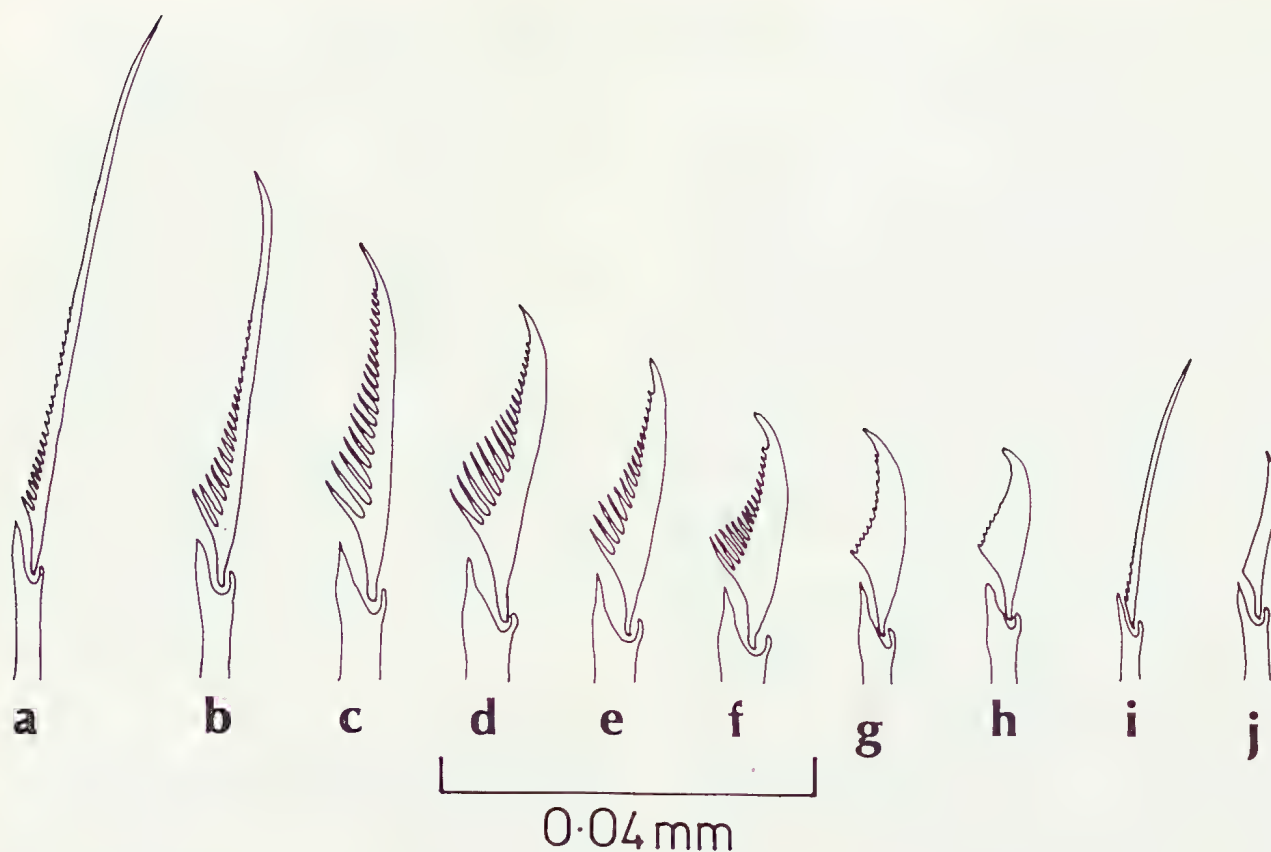


Fig. 24a-j. *P. psamathe*, setiger 32, neurosetal units (Holotype USNM 97850).

Chrysopetalum sp. were found with *P. psamathe* (USNM 97852).

Habitat. A collection of ten polychaete families from Punta Cholla included *P. psamathe* (AHF N 14112) and a number of terebellid and chaetopterid tube dwellers. Habitat data for polychaetes collected two days later from the same locality is recorded in the AHF register as 'sand and shell, encrusted tubes'. All Gulf of California collecting sites are around Cholla, Sonora which is located at the northeast end of the Gulf. A distribution map of sediments within the Gulf of California characterize the Cholla sites as silt and sand (Fauchald, 1979). Depth ranges from the intertidal to 18 m.

The more southwestern Mexico habitat is described as 'sand beneath rocks' at depths of 3–18 m. Gulf of Guayaquil material was located at a depth of 20 m.

Distribution. Gulf of California, Western Mexico and Ecuador.

Etymology. The species name, *psamathe*, is named after a nereid goddess of the sandy shore.

Paleaequor nicoyensis n. sp.

Figs 25–28

Material examined. HOLOTYPE: Central America, Costa Rica, Gulf of Nicoya, Stn 12, silt-clay and sand, 44 m, USNM 97484, coll. H. Dean, 11 July 1980; 52 setigers, 6.2 mm length,

1.2 mm width, specimen entire with damaged pygidial segment.

PARATYPES: Gulf of Nicoya, 2, USNM 97485; 3, AHF 1434; 13, NTM W. 1906. Range of specimens from 22 setigers, 2.7 mm length, 1.0 mm width to 37 setigers, 3.8 mm length, 1.06 mm width; both NTM W.1906.

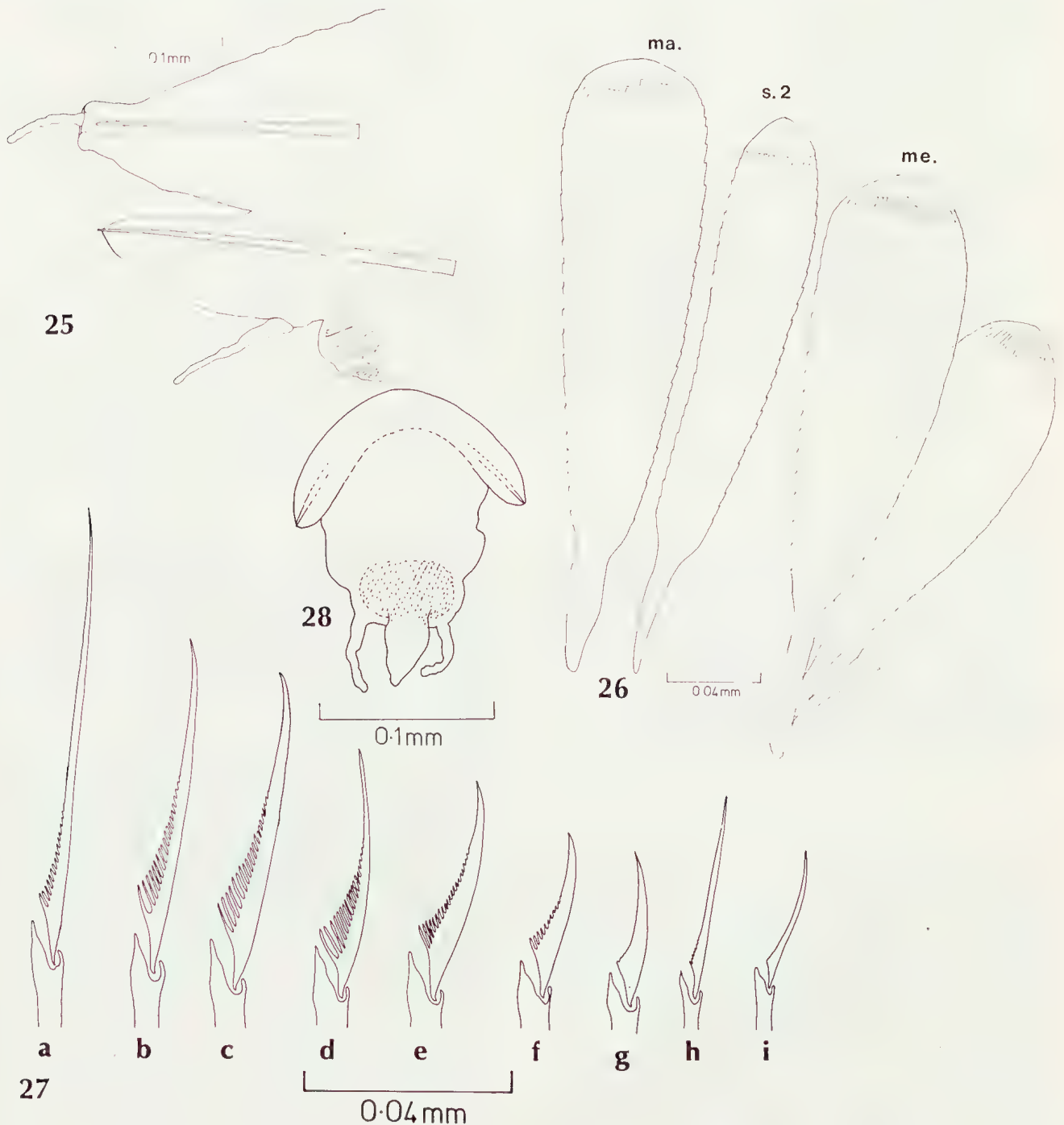
Description. Holotype with anterior segments relaxed. Prostomial and peristomial appendages visible. Two pairs of red-brown eyes visible anterior to nuchal fold. Notosetae comprising: 3–4 lateral paleae with 4–8 ribs; 1–2 slender paleae with 9–15 ribs inserted between lateral and main groups; up to 14 main paleae with 16–20 ribs and 3–5 raised and finely serrated ribs; 3–4 median paleae with 13–21 ribs and 0–4 raised ribs, 2 most distal median paleae with 17–21 ribs, 2 most proximal with 13–16 ribs. One small, slender palea (approximately $\frac{3}{4}$ length of main paleae) with 11–13 ribs and 2–3 raised ribs inserting between the main and median groups on posterior 10 setigers (Fig. 26). Small, fine granules on superior surface of main and distal median paleae. Paleae with very close set horizontal striae.

Narrow, pointed neuropodium with long, subulate ventral cirrus (Fig. 25). First and second neuropodia with neurosetae spinigers only. Subsequent neurosetae with superior group of 2 spinigers with slim shafts and long blades (Fig. 27a) present on each setiger to mid-body region. Posterior setigers have up to 3 spinigers including 1 with a short, fine blade (Fig. 27h). Mid-superior group of up to 8 falcigers, comprising 2 with

long blades (Fig. 27b), the others medium length blades with coarse basal serration (Fig. 27c,d). Mid-inferior group of 8–10 falcigers with medium to short length blades and coarse to fine basal serration (Fig. 27e,f). Inferior group of 4–5 falcigers with slender, short shafts and narrow, distally curved blades with fine to very fine basal serration (Fig. 27g). A single falciger with a very slim blade (almost spinigerous) included within inferior group in posterior 10 setigers (Fig. 27i). Pygidium

damaged in holotype; pygidium of paratypes composed of a rounded dorsal structure with two anal cirri and a slim, ventral cone (Fig. 28).

Habitat. A number of chrysopetalids were made available from samples from a benthic survey carried out in the Gulf of Nicoya, Costa Rica (Maurer, 1984). Specimens of *P. nicoyensis* were present in a number of stations located off the mouths of the Rio Barranca



Figs 25–28. *P. nicoyensis*: 25, setiger 25, dorsal view (Holotype USNM 97484); 26, setiger 49, proximal main palea (ma.), subunit 2 palea (s.2), median paleae (me.) (Holotype USNM 97484); 27a–i, setiger 29, neurosetal units (Paratype USNM 97485); 28, pygidium, ventral view (Paratype NTM W.1906).

Table 4. Comparison of setal counts between five *Paleaequor* species

Species	<i>P. setula</i>	<i>P. breve</i>	<i>P. heteroseta</i>	<i>P. psamathe</i>	<i>P. nicoyensis</i>
Pygidium					
1. quadrate without anal cone	1	1	2	2	2
2. rounded with anal cone					
Notosetal characteristics					
Lateral paleae (number)	4-7(8)	3-4	4	3-4	4
Number of ribs	2-5	2-4	4-9	4-7	4-8
Main paleae (number of ribs)	17-22(24)	17-20	17-22(24)	17-21	17-19
Median paleae (number)	2-3	2-3	3-4	3-4	3-4
Number of ribs (distal)	13-22	16-20	20-25	20-24(26)	16-20
Numbers of ribs (proximal)	9-12	8-16	11-20	13-18	13-16
Posterior position of single palea (sub-unit 2) within:					
1. posterior 10 setigers	1	1	2	2	1
2. posterior half of body					
Neurosetal characteristics					
Superior spinigers (number mid-body)	4	4	2	2	2
Mid-superior falcigers (number of long falcigers only)	2	2	2	0-1	2
Mid-superior falcigers (number)	6	6	5	4-5	6
Mid-inferior falcigers (number)	6-10	6-9	8-12	8-10	8-10
Inferior neurosetal type:					
1. spinigers	1	1	2	2	2
2. falcigers					
Inferior neurosetae (number)	4-5	5-7	4-6	3-5	4-5
Distribution (Fig. 1)	Australia: Queensland, Northern Territory, Papua-New Guinea	Vietnam: South Vietnam	Eastern United States: Southern Virginia to Gulf of Mexico	Mexico: Gulf of California, Western Mexico, Ecuador	Central America (Pacific): Costa Rica

and Rio Grande de Tarcoles. These are situated in the lower eastern Gulf, characterized by a shallow sandy silt shelf. Sediments recorded from individual stations range from sand to silt-clay with a high organic content associated with the latter. Depth ranges from 13 to 46 m.

Distribution. Pacific coast of Costa Rica.

Etymology. The species name, *nicoyensis*, is derived from the type locality (Gulf of Nicoya).

General Discussion

The five species of *Paleaequor* fall into two distinct morphological groups; group A (*P. setula*, *P. breve*) occurs in the western Pacific, and group B (*P. heteroseta*, *P. psamathe*, *P. nicoyensis*) occurs in the eastern Pacific and western Atlantic. Table 4 summarizes the character states for all species. The two species groups are separable on the basis of three characters, the states or values of which are constant within each group but differ between the two groups. Species in group A possess a quadrate pygidium, narrow lateral paleae with a low number of ribs, and inferior neurosetae composed of spinigers. Species in group B possess a pygidium composed of a dorsal rounded structure and a ventral cone, lateral paleae with a higher number of ribs, and inferior neurosetae composed of

falcigers. There are two additional characters that separate group A and B. The numbers of superior spinigers and median paleae are constant on mid-body setigers between group A and B but the numbers of superior spinigers and median paleae on the most anterior and posterior setigers are within a similar range for all *Paleaequor* species.

Within group A, *P. setula* differs from *P. breve* in having a higher number of lateral paleae. When comparing the structure of the paleae in the two species, *P. setula* has more ribs on the main paleae and there are also more ribs on the distal median paleae than in *P. breve*. There are fewer inferior spinigerous neurosetae in *P. setula* and the blades of these also are shorter (0.024-0.028 mm versus 0.031-0.036 mm). *Paleaequor setula* has higher numbers of lateral paleae than all other *Paleaequor* species.

Within group B (Americas), the relationship of the western Atlantic species (*P. heteroseta*) to the two American Pacific species (*P. psamathe* and *P. nicoyensis*) is equivocal. The composition and rib number of the three paleae types is similar in *P. heteroseta* and *P. psamathe* but the composition of the neurosetal fascicles in these species differs. *Paleaequor heteroseta* has larger, more robust neurosetae and higher numbers of mid-superior, long-bladed falcigers and inferior neurosetae. *P. heteroseta* shares similar

neurosetal characters with *P. nicoyensis* but the composition of the notosetal fascicles differ. *Paleaequor heteroseta* has broad proximal main and distal median paleae with a higher number of ribs and a single palea (subunit 2) located within the posterior half of the body.

In comparison with *P. heteroseta* and *P. nicoyensis* the northern and southern populations of *P. psamathe* possess short, conical neuropodia and relatively short-bladed spinigerous and falcigerous neurosetae. *Paleaequor psamathe* lacks, or has small numbers of long-bladed mid-superior falcigers and small numbers of inferior falcigers. *Paleaequor psamathe* differs greatly from *P. nicoyensis* in both notosetal and neurosetal characters; the fact that these two species are most dissimilar is of interest as *P. nicoyensis* is located in the middle of the range of distribution of *P. psamathe*.

Paleaequor nicoyensis is distinguished from *P. psamathe* and *P. heteroseta* by lower numbers of ribs in the main and median paleae; finer raised rib ornamentation and a finer granular sculpture on the main paleae; and the position of the single palea (subunit 2) within the posterior 10 setigers. It is further distinguished by having longer, narrower blades of the mid-inferior falcigers, and two types of inferior neurosetae (falcigerous and near spinigerous) within the posterior 10 setigers. In comparison with the other two American species, the rounded dorsal part of the pygidium in *P. nicoyensis* is retracted so that the two anal cirri extend laterally rather than posteriorly to the slim, ventral cone. While *P. nicoyensis* appears most closely related to its American congeners it also exhibits characters linking it to the western Pacific species. *Paleaequor nicoyensis* share with *P. setula* and *P. breve* a lower rib number on the distal median paleae; the position of the single palea within the posterior 10 setigers; and the presence of an inferior, almost spinigerous neuroseta within the posterior 10 setigers. It further shares with *P. breve* a similar number of ribs in the main and distal median paleae; fine raised rib ornamentation and a very fine granular sculptured superior surface on the main paleae.

Certain setal patterns, related to tapered body form, are persistent, i.e. present in all members of the genus, e.g. (1) certain setal types present in the mid-body increase, decrease or are absent at the anterior and posterior ends; (2) certain setal types are only present at the anterior or posterior end.

Certain setal characters in *Paleaequor* appear to be morphologically labile. This is evident by variation within and between individuals of a species in the type and number of setae throughout the body length. Similar variation also occurs between species, particularly variation in superior spiniger number, mid-superior upper falciger type and number, and type and number of inferior neurosetae. Setal variation between species is also seen in the number of median and lateral paleae, the number of ribs on the median and lateral paleae, and in the location of the single palea (subunit 2). Much of the variation in setal numbers and setal

morphology is difficult to interpret, particularly without outgroup comparisons, and it remains unclear whether the evolutionary changes in setal characters in *Paleaequor* involves principally loss or acquisition.

ACKNOWLEDGEMENTS. I am indebted to Hannelore Paxton, Jan Carey and Judell, Platt, Thomas & Assoc. Pty. Ltd. for access to specimens from the Queensland Nickel Survey. I thank Harlan Dean and Jan Watson for their generous gifts of specimens from Costa Rica and Papua New Guinea respectively. Thanks are due to the following individuals for the loan of specimens: Kristian Fauchald (USNM), Gordon Hendler (SOSC), Pat Hutchings (AM), Pat Mather and Stephen Cook (QM), Jeanne Renaud-Mornant (MNHN), Barbara Weitbrecht (CAS), and Sue Williams (AHF). I thank Jan Carey and Jan Watson for sediment data, and also the staff at the SEM unit, Smithsonian Institution, and Sue Doyle, Macquarie University, for the SEM photographs. I am most grateful to the Northern Territory Museum for funds to complete part of this study and in particular to Russell Hanley and Barry Russell who offered support and encouragement. Kristian Fauchald, Pat Hutchings, Barry Russell and an anonymous reviewer offered valuable advice on the manuscript. Many thanks are due to Jeannie Sindalle, Debra Hadfield, Lorna Watt and Chris Haigh for their patient typing of the manuscript.

References

- Carey, J., 1981. Nickel mining and refinery wastes in coral reef environs. Proceedings 4th International Coral Reef Symposium, Manila, Philippines, Vol. 1: 1-725.
- Day, J.H., 1973. New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. NOAA Technical Report NMFS CIRC-375 July 1973: 1-140.
- Ehlers, E., 1864. Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt. Engelmann, Leipzig: 1-268.
- Fauchald, K., 1969. Zoogeography and ecology of polychaetous Annelids of the Super-Family Eunicea off Western Mexico. Ph.D. Dissertation, University of Southern California.
- Gardiner, S.L., 1982. Errant polychaete annelids from North Carolina. Journal of the Elisha Mitchell Scientific Society 91(3): 78-220.
- Gathof, J., 1984. Chrysopetalidae, Vol. 3, Chapter 26. In 'Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico. Final Report to the Minerals Management Service' (eds J.M. Uebelaker & P.G. Johnson). Barry A. Vittor & Associates, Inc., Mobile, Alabama. 7 vols.
- Gallardo, V.A., 1968. Polychaeta from the Bay of Nha Trang, South Vietnam. Naga Report 4(3): 35-279, pls 1-59.
- Gibbs, P.E., 1971. The Polychaeta fauna of the Solomon Islands. Bulletin of The British Museum (Natural History) Zoology 21(5):101-211.
- Hartman, O., 1945. The marine annelids of North Carolina. Duke University Marine Station Bulletin 2: 1-54, pls 1-10.
- Horst, R., 1917. Polychaeta Errantia of the Siboga Expedition. Part 2. Aphroditidae and Chrysopetalidae. Siboga Expedition. Leyden 246: 1-140.
- Jorge, A.R., 1954. Contribution à l'étude des Chrysopétaliens I. Sur le prostomium et les premiers segments chez les

- genres *Chrysopetalum*, *Heteropale* et *Bhawania*. Revista da Faculdade de Ciências de l'Universit  de Lisboa, 2nd Serie, C. 4: 159-178.
- Levinsen, G.M.R., 1879. Om to nye slaegter af arctiske chaetopode Annelider. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening Kjobenhavn, 1879-1880: 9-18.
- Maurer, D. & J.A. Vargas, 1984. Diversity of soft-bottom benthos in a tropical estuary: Gulf of Nicoya, Costa Rica. Marine Biology 81: 97-106.
- Mileikovsky, S.A., 1962. On the morphology and systematics of polychaets belonging to the family Chrysopetalidae E. Ehlers, 1864 (genera *Paleanotus* L. Schmarda, 1861, *Heteropale* H.P. Johnson, 1897 and others). Zoologicheskii Zhurnal 41(5): 648-659 (in Russian with English resume).
- Orensanz, J.M., 1972. Los anelidos poliquetos de la provincia biogeografica Argentina. I. Palmyridae (= Chrysopetalidae), Amphinomidae y Euprosinidae. Physis, Buenos Aires 31(83): 485-501.
- Perkins, T.H., 1985. *Chrysopetalum*, *Bhawania* and two new genera of Chrysopetalidae (Polychaeta), principally from Florida. Proceedings of the Biological Society of Washington 98(4): 856-915.
- Potts, F.A., 1910. Polychaeta of the Indian Ocean. Part 2. The Palmyridae, Aphroditidae, Polynoidae, Acoetidae and Sigalionidae. Transactions Linnean Society of London, Zoology (2) 16: 325-353, pls 18-21.
- Renaud, J.C., 1956. A report on some polychaetous annelids from the Miami-Bimini area. American Museum Novitates 1812: 1-40.
- Rullier, F., 1964. Campagne de la Calypso: Iles du Cape Vert. 5. Ann lides Polych tes. Annales de l'Institut Oceanographique 41: 113-218.
- Schmarda, L.K., 1861. Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857. Vol. 1. Rotatorien und Anneliden. Leipzig, 164 pp.
- Shin, P.K.S., 1980. Some polychaetous annelids from Hong Kong Waters. In 'Proceedings 1st International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China' (eds B.S. Morton & C.K. Tseng). Vol. 1: 1-554. Hong Kong.
- Stephenson, W., Y.I. Raphael & S.D. Cook, 1976. The macrobenthos of Bramble Bay, Moreton Bay, Queensland. Memoirs of the Queensland Museum 17(3): 425-447.
- Wilson, W.H. Jr., 1979. Community structure and species diversity of the sedimentary reefs constructed by *Petaloproctus socialis* (Polychaeta: Maldanidae). Journal of Marine Research 37(4): 623-641.

RECORDS OF THE AUSTRALIAN MUSEUM

VOLUME 38 No. 4

A review of the parrotfishes (family Scaridae) of the Great Barrier Reef of
Australia with description of a new species J. HOWARD CHOAT
AND JOHN E. RANDALL

175

A Review of the Parrotfishes (Family Scaridae) of the Great Barrier Reef of Australia with Description of a New Species

J. HOWARD CHOAT^a AND JOHN E. RANDALL^b

^aDepartment of Zoology, University of Auckland, PB Auckland, New Zealand*

^bBishop Museum, Box 19000-A, Honolulu, Hawaii 96817, USA.

ABSTRACT. The family Scaridae is represented on the tropical and subtropical coasts of eastern Australia by 25 previously described species. Three species belong in the subfamily Sparisomatinae: *Leptoscarus vaigiensis* (Quoy & Gaimard); *Calotomus carolinus* (Valenciennes); *Calotomus spinidens* (Quoy & Gaimard). The remainder are included in the subfamily Scarinae: *Bolbometopon muricatum* (Valenciennes); *Cetoscarus bicolor* (Rüppell); *Hipposcarus longiceps* (Valenciennes); *Scarus altipinnis* (Steindachner); *Scarus bleekeri* (de Beaufort); *Scarus dimidiatus* Bleeker; *Scarus flavipectoralis* Schultz; *Scarus forsteni* (Bleeker); *Scarus frenatus* Lacepède; *Scarus frontalis* Valenciennes; *Scarus ghobban* Forsskål; *Scarus gibbus* Rüppell; *Scarus globiceps* Valenciennes; *Scarus longipinnis* Randall & Choat; *Scarus niger* Forsskål; *Scarus oviceps* Valenciennes; *Scarus psittacus* Forsskål; *Scarus pyrrhurus* (Jordan & Seale); *Scarus rivulatus* Valenciennes; *Scarus rubroviolaceus* Bleeker; *Scarus schlegeli* (Bleeker); *Scarus sordidus* Forsskål; *Scarus spinus* Kner. The scarid from Australian waters previously misidentified as *Scarus lunula* (a synonym of *Scarus festivus* Valenciennes) represents an undescribed species *Scarus chameleon*, described herein. *Scarus chameleon* has a distribution that includes the western and southern Pacific. It is similar to *S. festivus* but differs in patterns of head and body colouration in the terminal phase, and in the head profile. All but three species listed above are most commonly encountered on the coral reefs of the Great Barrier Reef and the adjacent coral sea. The exceptions are the sparisomatine species *Leptoscarus vaigiensis* and *Calotomus spinidens*, and the scarinine species *Scarus ghobban*. The former two species are often associated with seagrass beds in coastal areas, while *Scarus ghobban* frequents a variety of non-reef habitats. Many of the species listed extend into northern and western Australian waters. Additional collecting is required to establish the limits and identities of the entire Australian scarid fauna. Colour photographs of fresh specimens illustrating the different colour phases of all 27 species are provided. In addition, underwater colour photographs of most species are provided with an emphasis on those which show confusing patterns of short term variation in the initial colour phase. Illustrations of the juvenile phase are provided for some species.

CHOAT, J.H. & J.E. RANDALL, 1986. A review of the parrotfishes (Family Scaridae) of the Great Barrier Reef of Australia, with description of a new species. Records of the Australian Museum 38(4): 175–239.

CONTENTS

Abstract	175
Introduction	176
Materials and Methods	177
Historical Review and Nomenclature of Australian Species	179
Zoogeography and Distribution	184
Colour Phases and Reproduction	188
Key to the Scarids of the Great Barrier Reef	189

*Present Address: Department of Marine Biology, James Cook University, Townsville, 4811, Australia

<i>Calotomus carolinus</i> (Valenciennes)	193
<i>Calotomus spinidens</i> (Quoy & Gaimard)	194
<i>Leptoscarus vaigiensis</i> (Quoy & Gaimard)	194
<i>Cetoscarus bicolor</i> (Rüppell)	195
<i>Hipposcarus longiceps</i> (Valenciennes)	196
<i>Bolbometopon muricatum</i> (Valenciennes)	197
<i>Scarus altipinnis</i> (Steindachner)	198
<i>Scarus bleekeri</i> (De Beaufort)	199
<i>Scarus chameleon</i> n.sp.	199
<i>Scarus dimidiatus</i> Bleeker	203
<i>Scarus flavipectoralis</i> Schultz	204
<i>Scarus forsteni</i> (Bleeker)	204
<i>Scarus frenatus</i> Lacepède	205
<i>Scarus frontalis</i> Valenciennes	206
<i>Scarus ghobban</i> (Forsskål)	207
<i>Scarus gibbus</i> Rüppell	209
<i>Scarus globiceps</i> Valenciennes	210
<i>Scarus longipinnis</i> Randall & Choat	211
<i>Scarus niger</i> (Forsskål)	213
<i>Scarus oviceps</i> Valenciennes	214
<i>Scarus psittacus</i> (Forsskål)	215
<i>Scarus pyrrhurus</i> (Jordan & Seale)	216
<i>Scarus rivulatus</i> Valenciennes	217
<i>Scarus rubroviolaceus</i> Bleeker	219
<i>Scarus schlegeli</i> (Bleeker)	220
<i>Scarus sordidus</i> (Forsskål)	221
<i>Scarus spinus</i> (Kner)	222
Acknowledgements	223
References	223

The Scaridae, a family of labroid fishes, are highly characteristic of coral reef habitats. With few exceptions their geographical distribution is linked to that of tropical reef environments. The number of species of scarids is not great when compared with other families of tropical perciform fishes. However, their relatively large size, complex patterns of colour change, and conspicuous grazing habit have resulted in a continuing interest in this group by ichthyologists and reef biologists generally.

All members of the family Scaridae possess a continuous dorsal fin with 9 flexible spines and 10 soft rays, and an anal fin with 3 flexible spines and 9 soft rays; pectoral fins have 2 unbranched rays (the first always rudimentary) and 11–15 branched rays. Body scales are always large and cycloid with 22–24 in the lateral line. There are 1–4 rows of cheek scales with varying numbers of scales in each row and 2–8 median predorsal scales. Gill rakers of scarids show considerable variation both within and between species. The number of gill rakers within a species will also vary with the size of the individual.

Important structural and ecological characters are the fusion of teeth to form beak-like dental plates, a pharyngeal apparatus in which flattened teeth form a grinding mill, the absence of a true stomach, and a herbivorous habit. A minority of species selectively graze living corals. The scarids form a natural grouping

both taxonomically and ecologically and we prefer to maintain this distinction at the familial level. We do not accept the argument of Kaufman & Liem (1982) that places the Labridae and Scaridae within the same family.

We follow Bruce & Randall (1985) in recognizing two subfamilies of Scaridae, the Sparisomatinae which includes the genera *Leptoscarus* and *Calotomus*, and the Scarinae. The latter subfamily includes all the species characteristic of reef environments and constitutes the main focus of this review. Sparisomatine parrotfishes are more likely to be encountered in non-reef environments such as seagrass beds and are not important members of the Great Barrier Reef fauna. Very few sparisomatine parrotfishes were observed or collected from eastern Australia. For structural details of the three Australian species in this subfamily the reader is referred to the recent revision, Bruce & Randall (1985).

The generic classification of the Scarinae used here follows that of Randall & Bruce (1983). The genus *Bolbometopon* Smith is restricted to a single species, *muricatum*; *Scarus bicolor* Rüppell is placed in *Cetoscarus*. We recognize *Hipposcarus* Smith as a valid genus for *Scarus longiceps* Valenciennes and refer the genus *Scarops* Schultz to the synonymy of *Scarus* Forsskål.

Scarids are important members of reef communities

and have been the focus of a number of questions concerning the importance of herbivorous feeding on reefs and the biology of reef fishes generally, (Choat & Bellwood, 1986; Hatcher & Larkum, 1983; Russ, 1984a,b). Reliable identifications of scarid fishes are a prerequisite for many of these studies. Such identification may be a difficult task. All species are very similar in external morphology and meristic features. They have the same number of lateral line scales, the same number of spines and rays in the medial fins, and very similar body proportions. Some meristic characters, including the number of pectoral rays, the number of scale rows and scales on the cheek, and the number of median predorsal scales vary amongst species. However the diagnostic value of such variation may be limited, as it separates scarids into species groups rather than individual species.

Colour pattern is an important character for distinguishing species of scarids but the use of colour as a diagnostic feature requires caution. Most colour fades rapidly on death and under conditions of preservation may bear little relation to life features, although some distinguishing markings are retained. More importantly the majority of scarids undergo a complex sequence of colour changes during their life. These changes are linked to growth and patterns of sexual ontogeny, most species being protogynous hermaphrodites (Choat & Robertson, 1975).

Previous attempts to review the taxonomy of scarids (Smith, 1956, 1959; Schultz, 1958, 1969) suffered from a lack of information on patterns of colour change, and the poor state of preservation of much of the type material. This has been discussed in detail elsewhere (Randall, 1963; Randall & Choat, 1980; Randall & Bruce, 1983; Bruce & Randall, 1985). These more recent studies with an emphasis on field work have provided two elements essential to a better understanding of scarid taxonomy, good descriptions of the character and sequence of colour change, and a more rigorous analysis of scarid distribution patterns.

The present study provides for the identification of scarids within a single tropical region, the Great Barrier Reef off north-eastern Australia. Although some species have very broad distributions, there are distinct regional groupings of scarids within the western Indian Ocean, the Indo-West and central Pacific (Randall & Bruce, 1983). A study of a major reef area in the southern Pacific provides the material for biogeographic comparisons with other areas such as the northern tropical Pacific (Masuda et al., 1984), the western Indian Ocean and the Red Sea (Randall & Bruce, 1983), and the eastern Pacific (Rosenblatt & Hobson, 1969). In addition the geographic situation of the Great Barrier Reef itself with combined latitudinal (11°S to 22°S) and habitat (coastal mangrove forests to Coral Sea reefs) variation provides a good opportunity for analysing species distributions with reference to these factors (Williams, 1982; Williams & Hatcher, 1983). Other Australian regions, especially the reefs of the northern and north-west coasts, require additional collecting.

Material available to date suggests that these reefs cannot be considered simply as extensions of the Great Barrier Reef.

This study emphasizes life colouration of scarids in the initial and terminal colour phases for each species and deals mainly with the adults. An important aspect of scarid biology, the identification of individuals newly recruited to the reef, will be dealt with in a separate publication. The present work does consider juvenile colouration in species where the phase is particularly striking and likely to be encountered by divers. Our concern is with the upper end of the juvenile size range and adults. Bellwood & Choat (in prep.) will consider very small individuals at the lower end of the juvenile size range.

Introductory aspects of scarid taxonomy and biology are considered under separate headings. These include historical aspects of scarid taxonomy in the Australian region, and distribution patterns of scarid faunas.

Materials and Methods

For species descriptions the emphasis is on the colour of living and fresh material in the initial phase (IP) and terminal phase (TP). Where juveniles are known to have distinct colour phases these are also included; greater detail of colour pattern in small scarids will be provided elsewhere (Bellwood & Choat, in prep.). In this study the term juvenile refers to individuals not sexually mature and usually between 50–120 mm standard length (SL). Where sexual identity is specified this was determined histologically. The majority of species examined are protogynous hermaphrodites; exceptions are identified. The term IP refers to subadult and adult females, primary males and occasionally small secondary males. TP phase refers to secondary males. In colour descriptions, stripes are longitudinal bands, bars are vertical markings.

Meristic data include the number of median predorsal scales, the number of cheek scale rows, the number of scales in each of these rows, and the number of pectoral fin rays. Median predorsal scales are counted from the most anterior scale; small lateral or overlapping scales anterior to the first median predorsal are identified but not included in the counts. Scale rows on the cheek are the horizontal rows between the lower edge of the orbit and the lower margin of the preopercle. The counts of scales in each row start at the most anterior scale (Fig. 1) and do not include the single large postorbital scale characteristic of most species. Counts of the pectoral rays include the upper rudimentary ray which is unbranched. No distinction is made between the upper two unbranched rays and the remaining branched rays. The last dorsal and anal fin rays are split to their base but counted as a single rays. Gill rakers are useful for separating genera of scarids and the species within the subfamily Sparisomatinae (Bruce & Randall, 1983). Gill rakers within the subfamily Scarinae were found to vary both intra- and interspecifically especially in the genus

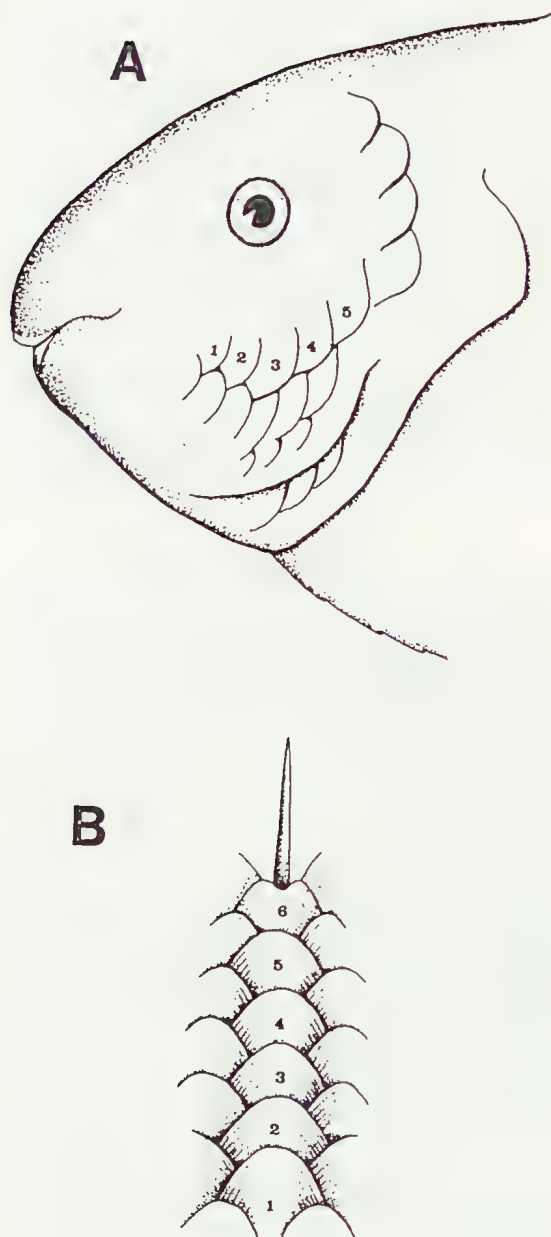


Fig. 1. A, format used for counting cheek scales. There are 3 rows of cheek scales with 5 scales in the upper row. Scales are counted with the anterior scale first. The large postorbital scale is not included in the cheek scale counts. B, format used for counting median predorsal scales; there are 6 median predorsal scales with the anterior scale counted first. The 2 smaller scales on each side of the first scale are not included in the counts. Scale size is measured as the distance between the posterior tip of one scale and the next. For the first scale the measure is from the base of the scale to its posterior tip.

Scarus. Gill-raker counts were not recorded from members of this genus. The numbers of canine teeth were found to have some diagnostic value and are included. Meristic material in the diagnoses and Tables 1 to 3 refers to Great Barrier Reef material unless specified.

Table 1. Counts of median predorsal scales in Great Barrier Reef scarids.

Species	3	4	5	6	7	8
<i>L. vaigiensis</i>		4				
<i>B. muricatum</i>	1	1	1			
<i>C. bicolor</i>		2	2	3	1	
<i>H. longiceps</i>		13				
<i>S. gibbus</i>		19	1			
<i>S. flavipectoralis</i>	1	14				
<i>S. schlegeli</i>		37				
<i>S. psittacus</i>		50				
<i>S. sordidus</i>		41				
<i>S. spinus</i>	2	20	3			
<i>S. chameleon</i>		39	3			
<i>S. bleekeri</i>		9				
<i>S. longipinnis</i>	2	4				
<i>S. rubroviolaceus</i>				5		
<i>S. dimidiatus</i>			1	2		
<i>S. oviceps</i>			1	13	1	
<i>S. globiceps</i>			34	24	4	
<i>S. rivulatus</i>			10	42	6	
<i>S. ghobban</i>			2	36		
<i>S. altipinnis</i>			2	14		
<i>S. forsteni</i>			2	6	1	
<i>S. frenatus</i>				9	6	
<i>S. niger</i>					5	9

Table 2. Pectoral fin rays (counts from both sides of fish)

Species	13	14	15	16	17
<i>L. vaigiensis</i>	8				
<i>B. muricatum</i>				6	
<i>C. bicolor</i>	1	14	1		
<i>H. longiceps</i>		2	24		
<i>S. gibbus</i>		2	34	2	
<i>S. flavipectoralis</i>		30			
<i>S. schlegeli</i>	2	63	9		
<i>S. psittacus</i>	1	96	3		
<i>S. sordidus</i>		4	76		
<i>S. spinus</i>	5	43			
<i>S. chameleon</i>	3	80	3		
<i>S. bleekeri</i>		1	15		
<i>S. longipinnis</i>		11	1		
<i>S. rubroviolaceus</i>			8	2	
<i>S. dimidiatus</i>		6			
<i>S. oviceps</i>		28	2		
<i>S. globiceps</i>		129	11		
<i>S. rivulatus</i>	3	92	19		
<i>S. ghobban</i>		4	71	3	
<i>S. altipinnis</i>		1	30	1	
<i>S. forsteni</i>	2	16			
<i>S. frenatus</i>		21	9		
<i>S. niger</i>		31	1		

Table 3. Counts of cheek scales in each row (counts from both sides of fish)

Species	Row 1					Row 2				
	4	5	6	7	8	4	5	6	7	8 9
<i>L. vaigiensis</i>	8									
<i>B. muricatum</i>	1	2	3			3	3			
<i>C. bicolor</i>				3	3			1	3	2
<i>H. longiceps</i>		1	4	4	1			1	4	5
<i>S. gibbus</i>		3	10	7		4	9	7		
<i>S. flavipectoralis</i>			21	11		1	4	21	6	
<i>S. schlegeli</i>		3	42	20	1		7	42	16	1
<i>S. psittacus</i>	1	10	79	10			4	19	64	5
<i>S. sordidus</i>		14	54	10	2		10	38	36	
<i>S. spinus</i>		34	13	1			23	15	9	1
<i>S. chameleon</i>		7	57	12			2	40	33	1
<i>S. bleekeri</i>			10	5	1			5	6	5
<i>S. longipinnis</i>	1	7	4			2	5	5		
<i>S. rubroviolaceus</i>			8	2				4	6	
<i>S. dimidiatus</i>			3	3				2	3	1
<i>S. oviceps</i>	1	7	2					3	5	1 3
<i>S. globiceps</i>	9	78	48					28	78	31 1
<i>S. rivulatus</i>	19	85	8			6	74	27	1	
<i>S. ghobban</i>	5	64	3			6	61	5		
<i>S. altipinnis</i>	1	9	6				3	9	4	
<i>S. forsteni</i>	1	8	3				1	5	5	1
<i>S. frenatus</i>	1	16	11				2	8	18	
<i>S. niger</i>	2	12	14				5	8	10	3

Table 3. Cheek scales (continued)

Species	Row 3						
	1	2	3	4	5	6	7
<i>B. muricatum</i>	4	2					
<i>C. bicolor</i>			1	1	3	1	
<i>H. longiceps</i>		1	1	2	5	1	
<i>S. gibbus</i>		1	1	7	8	3	
<i>S. flavipectoralis</i>	19	11					
<i>S. spinus</i>	4	39	5				
<i>S. chameleon</i>	11	56	18				
<i>S. longipinnis</i>		12					
<i>S. rubroviolaceus</i>		4	6				
<i>S. dimidiatus</i>	1	3	2				
<i>S. oviceps</i>	1	5	4				
<i>S. globiceps</i>	4	47	81	9			
<i>S. rivulatus</i>	8	102	10				
<i>S. ghobban</i>	14	52	10				
<i>S. altipinnis</i>	2	19	11				
<i>S. forsteni</i>		2	8	3	3		
<i>S. frenatus</i>		10	7	11			
<i>S. niger</i>		15	10	5			

Proportional measurements are used in some instances to separate species but these are not generally diagnostic. Unless specified, length refers to standard length, the straight-line distance from front of snout to base of caudal fin (end of hypurals). Head length is taken from the same anterior point to the posterior fleshy end of the operculum. Depth of the body is the greatest depth. Width of the body is the maximum width immediately posterior to the head. Orbit width is the

greatest fleshy diameter. Interorbital width is the least bony width. Caudal peduncle depth is the least depth. The length of the caudal peduncle is the horizontal distance between the insertion of the last anal ray and the base of the caudal fin. The dorsal and anal spines and rays are usually curved; their lengths are straight-line measurements from extreme base to distal end. Caudal fin length is the greatest horizontal length. Caudal concavity is the horizontal distance between verticals at the tips of the longest and shortest rays of species with emarginate or lunate caudal fins. Pelvic fin length is from the base to the tip of the longest ray. In the description of the new species, data in parentheses refer to paratypes. Additional proportional measurements are provided in the relevant tables.

Both authors collected and observed scarids at the northern and southern ends of the Great Barrier Reef. The senior author was able to collect and observe on a series of central reefs from inshore to outer shelf habitats. In addition, a number of workers provided us with information on scarid distribution and abundance patterns from other areas of the Great Barrier Reef and a series of Coral Sea reefs. Unless indicated, the photographs were taken by the junior author. In some instances suitable photographs of Great Barrier Reef material were not available. Under these circumstances, photographs of the species in question from other localities within the species range were used. The locality of each individual illustrated is shown in the figure legends.

In synonymies, the symbol . — separating a scientific name and an author indicates that this reference is not the original description of the species. The identity of scarids from regional lists within the Australian and New Guinea regions are matched as far as possible with current nomenclature. Distributions of each species within the Australian region are indicated, but more collecting in northern and western Australia will undoubtedly result in modifications to these.

Specimens were examined from and deposited in the Australian Museum (AMS); Queensland Museum (QM); West Australian Museum (WAM); Bernice P. Museum (BPBM); British Museum (Natural History) (BM(NH)); Smithsonian Institution, Washington (USNM); Museum National d'Histoire Naturelle (MNHN).

Species accounts are in alphabetical order. The key refers mainly to adult individuals of each species.

Historical Review and Nomenclature of Australian Species

Historically, the taxonomic study of Australian scarids has had two distinct periods. During the latter part of the nineteenth century a number of scarids were collected, mainly from north Queensland coastal waters; ten of these were identified as new species. A smaller number of species were recognized as wider ranging scarids and added to the Australian faunal lists. Very

few additional scarids were recorded until the development of SCUBA diving. Scarids did not feature in the major collecting and descriptive episodes of Ogilby, McCulloch and Whitley during the early and mid-periods of the twentieth century. This suggests difficulties both in collecting in reef environments and the uncertainties of identification of preserved scarid material. The checklists of McCulloch (1930) and Whitley (1964) reflect this. These lists have been augmented by a number of more recent publications. These include the popular text of Marshall (1965) and the illustrated checklist and key of the scarid fauna from the adjacent reefs of New Guinea (Munro, 1967).

The first attempt to compile a record of a Great Barrier Reef scarid fauna was the species list of Heron Island fishes by Woodland & Slack-Smith (1963). Australian Museum-sponsored expeditions by F.H. Talbot to the southern and northern ends of the Great Barrier Reef provided comprehensive species lists culminating in the checklist of fishes recorded from the Capricorn-Bunker reefs (Russell, 1983). This includes 23 species of scarids and differs from the present study only by the absence of recent records from northern waters (*S.pyrrhurus*, *S.frontalis*, *C.spinidens*), and *Bolbometopon muricatum* which is restricted to central and northern areas of the Great Barrier Reef. In addition, the work on scarid reproductive biology by Choat & Robertson (1975) provides a list of scarid species from Heron Island. The checklist of fishes from Lord Howe Island (Allen et al., 1976) provides records of Australian scarids near the southern extremity of their range.

The lists of McCulloch and Whitley provide an entry to the early literature on Australian scarids. They recorded new species described from Australian waters prior to 1964 and early additions to the Australian fauna. Both these categories are considered below.

Twelve species of scarids have been described from Australian waters, most of them from three collections made in the latter half of the nineteenth century. The following species were described as new: *Pseudoscarus viridescens* Castelnau, 1875; *P. obscurus* Castelnau, 1875; *P. modestus* Castelnau, 1875; *P. dumerilii* Castelnau, 1875; *P. richardsonii* Castelnau, 1875; *P. strigipinnis* De Vis, 1885; *P. fuscus* De Vis, 1885; *P. flavipinnis* De Vis, 1885; *P. flavolineatus* Alleyne & Macleay, 1877; *P. nudirostris* Alleyne & Macleay, 1877; *Scarus pyrrostethus australianus* Paradice & Whitley, 1927; and *Scarus toshi* Whitley, 1933. Schultz (1969), in a major review of parrotfishes, considered all of these to be unidentifiable with the exceptions of *S. pyrrostethus australianus* which was placed in the synonymy of *S. ghobban*, and *S. toshi* which he erroneously referred to *S. harid*.

The collections of scarids made by Castelnau resulted in the description of five new species. The type localities of two of these, *P. modestus* and *P. dumerilii*, were Adelaide, and the remaining three were from Cape York. The species from Adelaide are members of the family Odacidae (Gomon & Paxton, 1985) which have

a number of scarid-like features. Those from Cape York were almost certainly scarids but no type material can be located in any Australian museums or in the Paris Museum. The published descriptions are not sufficient to allow identification, and unless type material is located, *P. obscurus*, *P. richardsoni* and *P. viridescens* will remain unidentifiable.

Both De Vis and Alleyne & Macleay described a number of scarids collected in Australian waters. The types are in Australian museums and generally in good condition. De Vis (1885) described three species of scarids collected in north-eastern Australian waters, the types of which were examined in the Queensland Museum. These were found to represent the previously described *S. ghobban* and *S. globiceps* both of which are widely distributed in tropical waters. Alleyne & Macleay (1877) described two species from Cape Grenville, north Queensland. The types in good condition in the Australian Museum represent *S. rivulatus* and *S. ghobban*, previously described and widely distributed species.

Two further species described from Australian waters are *Scarus pyrrostethus australianus* Paradice & Whitley, 1927 and *Scarus toshi* Whitley, 1933. The type of the former is in the Australian Museum and is *S. ghobban*. Although no formally designated type of *S. toshi* exists, it is certain that this species also represents *S. ghobban*.

That most of the identifiable species of scarids described from Australian waters should be referred to *Scarus ghobban* is not surprising. Earlier workers did not have easy access to reef environments and those that did would have found most scarids difficult to collect. Species such as *S. ghobban* and *S. rivulatus* are representatives of the few scarid species which may occur in non-reef environments such as mangroves and rocky shores where they might have been collected by netting and spearing.

In addition to these new species there are a number of earlier records of scarids in the checklists of McCulloch and Whitley which require confirmation. These are *Scarus cyanotaenia* Bleeker, *Scarus axillaris* Steindachner, *Scarus gymnognathus* Bleeker, *Scarus octodon* Bleeker, and *Scarichthys auritus* Bleeker. *Scarus cyanotaenia* was erroneously used by Ogilby (1915) for *S. ghobban*. *Scarus axillaris*, a Caribbean species, is recorded from the 'north coast of Australia' but this is clearly erroneous (Schultz, 1958). Kner (1865) recorded *Pseudoscarus octodon* from Sydney but the description does not allow identification. *Scarus gymnognathus* is a synonym of *S. sordidus*, and *S. auritus* is a synonym of *L. vaigiensis*.

Table 4 lists the nominal species of scarids described from Australian waters and matches these with their present identification. Table 5 lists the nominal species of scarids recorded from Australian waters in a number of important regional studies and species lists. Information concerning the New Guinea scarid fauna is included for comparative purposes.

Table 4. List of nominal species of scarids described from Australian waters. The scientific name as it originally appeared, in alphabetical order according to the trivial name, the author and the date of publication and the present identification. Refer to the text under the senior synonym for the basis of determination.

Species, Author, Publication date	Present Identification
<i>Pseudoscarus dumerilii</i> Castelnau, 1875	<i>Siphonognathus radiatus</i> (Quoy & Gaimard) Family Odacidae
<i>Pseudoscarus flavipinnis</i> De Vis, 1885	<i>Scarus ghobban</i> Forsskal
<i>Pseudoscarus flavolineatus</i> Alleyne & Macleay, 1877	<i>Scarus rivulatus</i> Valenciennes
<i>Pseudoscarus fuscus</i> De Vis, 1885	<i>Scarus globiceps</i> Valenciennes
<i>Pseudoscarus modestus</i> Castelnau, 1875	<i>Odax acroptilus</i> (Richardson) Family Odacidae
<i>Pseudoscarus nudirostris</i> Alleyne & Macleay, 1877	<i>Scarus ghobban</i> Forsskal
<i>Pseudoscarus obscurus</i> Castelnau, 1875	Type not located
<i>Pseudoscarus richardsonii</i> Castelnau, 1875	Type not located
<i>Scarus pyrostethus australianus</i> Paradise & Whitley, 1927	<i>Scarus ghobban</i> Forsskal
<i>Pseudoscarus strigipinnis</i> De Vis, 1885	<i>Scarus globiceps</i> Valenciennes
<i>Callyodon toshi</i> Whitley, 1933	<i>Scarus ghobban</i> Forsskal
<i>Pseudoscarus viridescens</i> Castelnau, 1875	Type not located

In addition the types of a number of species of scarids described by Macleay (1883) with a type locality of Port Moresby were examined. These are included below.

<i>Pseudoscarus frontalis</i> Macleay 1883	<i>Scarus rubroviolaceus</i> Bleeker
<i>Pseudoscarus goldei</i> Macleay 1883	<i>Scarus sordidus</i> Forsskal
<i>Pseudoscarus labiosus</i> Macleay 1883	<i>Scarus psittacus</i> Forsskal
<i>Pseudoscarus moresbyensis</i> Macleay 1883	<i>Scarus quoyi</i> Val.
<i>Pseudoscarus papuensis</i> Macleay 1883	Type not located
<i>Pseudoscarus zonatus</i> Macleay 1883	<i>Scarus oviceps</i> Val.

Table 5. A list of the nominal species of scarids recorded from Australian waters in various checklists and from New Guinea by Munro (1967). We have used the checklists of (1) McCulloch (1930), (2) Woodland & Slack-Smith (1963), (3) Whitley (1964), (4) Marshall (1965) and (5) Russell (1983). Choat & Robertson (1975) provided a list (6) of scarids from the Capricorn-Bunker reef as a part of their study on scarid reproductive biology. In addition we have also included the species listed by (7) Munro (1967) from New Guinea waters. Many of these were recorded from southern New Guinea waters and probably have common distributions with the northern Great Barrier Reef fauna. In some instances the true identity of New Guinea material is uncertain. Allen et al. (1976) (8) provide a list of scarids from Lord Howe Island. For discussion refer to the text under the senior synonym.

GBR = Great Barrier Reef; Val. = Valenciennes

Scarid Identity and Checklist Record	Present Identification
<i>Callyodon aeruginosus</i> (Val.) New Guinea (7)	<i>Scarus rivulatus</i> Val.
<i>Scaricthys auritus</i> Valenciennes Moreton Bay, Lord Howe Is.(1)	<i>Leptoscarus vaigiensis</i> (Quoy & Gaimard)
<i>Scarus axillaris</i> Steindachner Northern Australia (1)	<i>Sparisoma rubripinnae</i> (Val.)
<i>Xanophon bataviensis</i> (Bleeker) New Guinea (7)	<i>Scarus psittacus</i> Forsskal
<i>Bolbometopon bicolor</i> (Rüppell) Heron Is. (6)	<i>Cetoscarus bicolor</i> (Rüppell)
<i>Cetoscarus bicolor</i> (Rüppell) Heron Is., GBR (2) (4) (5)	
<i>Chlorurus bicolor</i> (Rüppell) GBR (3)	
<i>Xanophon bleekeri</i> (de Beaufort) New Guinea (7)	<i>Scarus bleekeri</i> (de Beaufort)
<i>Scarus bleekeri</i> (de Beaufort) Southern GBR (5) (6)	

Scarid Identity and Checklist Record

Present Identification

<i>Callyodon blochi</i> (Val.) New Guinea (7)	<i>Scarus quoyi</i> Val.
<i>Scarus brevifilis</i> (Gunther) Southern GBR (5)	<i>Scarus altipinnis</i> (Steindachner)
<i>Calotomus carolinus</i> (Val.) Southern GBR (5)	<i>Calotomus carolinus</i> (Val.)
<i>Callyodon chlorodon</i> (Jenyns) New Guinea (7)	<i>Scarus altipinnis</i> (Steindachner)
<i>Scarus chlorodon</i> Jenyns Heron Is., Lord Howe Is. (6) (8)	
<i>Leptoscarus coeruleopunctatus</i> (Bleeker) Moreton Bay (4)	<i>Leptoscarus vaigiensis</i> (Quoy & Gaimard)
<i>Callyodon cyanognathus</i> (Bleeker) New Guinea (7)	<i>Scarus tricolor</i> Bleeker?
<i>Scarus cyanotaenia</i> Bleeker GBR and Moreton Bay (1) (4)	<i>Scarus ghobban</i> Forsskal
<i>Xanothron cyanotaenia</i> (Bleeker) Moreton Bay (3)	
<i>Scarus dimidiatus</i> Bleeker Southern GBR (5)	<i>Scarus dimidiatus</i> Bleeker
<i>Scarus dubius</i> Bennett Heron Is., GBR (2) (4)	<i>Scarus rivulatus</i> Val.
<i>Callyodon dubius</i> Bennett New Guinea (7)	<i>Scarus rivulatus</i> Val.?
<i>Xanothron erythrodon</i> (Val.) New Guinea (7)	<i>Scarus sordidus</i> Forsskal
<i>Scarus fasciatus</i> Val. Heron Is. (2) (6)	<i>Scarus rivulatus</i> Val.
<i>Callyodon fasciatus</i> Val. GBR, New Guinea (3) (4) (7)	
<i>Callyodon flavipectoralis</i> (Schultz) New Guinea (6)	<i>Scarus flavipectoralis</i> Schultz
<i>Scarus flavipectoralis</i> Schultz Southern GBR (5) (6)	
<i>Callyodon formosus</i> (Val.) GBR, New Guinea (3) (7)	<i>Scarus spinus</i> Kner
<i>Scarus formosus</i> Val. Heron Is. (6)	
<i>Callyodon forsteri</i> (Val.) GBR (3)	<i>Scarus psittacus</i> Forsskal
<i>Scarus forsteri</i> Val. Heron Is., Lord Howe Is. (6) (8)	
<i>Callyodon frenatus</i> (Lacepède) GBR (3)	<i>Scarus frenatus</i> Lacepède
<i>Scarus frenatus</i> Lacepède Southern GBR (5)	
<i>Scarus ghobban</i> Forsskal Heron Is., Lord Howe Is. (2) (5) (6) (8)	<i>Scarus ghobban</i> Forsskal
<i>Callyodon ghobban</i> (Forsskal) GBR, New Guinea (3) (7)	
<i>Scarus gibbus</i> Rüppell Southern GBR, Lord Howe Is. (5) (6) (8)	<i>Scarus gibbus</i> Rüppell
<i>Scarus globiceps</i> Val. Heron Is. (2) (5) (6)	<i>Scarus globiceps</i> Val.
<i>Callyodon globiceps</i> (Val.) GBR (3) (4)	
<i>Scarus gymnognathus</i> Bleeker Western Australia (1)	<i>Scarus sordidus</i> Forsskal
<i>Calotomus japonicus</i> (Val.) New Guinea (7)	<i>Calotomus spinidens</i> (Quoy & Gaimard)?
<i>Scarops jordani</i> (Jenkins) New Guinea (7)	<i>Scarus rubroviolaceus</i> Bleeker
<i>Scarus lepidus</i> Jenyns Heron Is. (6)	<i>Scarus forsteni</i> Bleeker

Scarid Identity and Checklist Record	Present Identification
<i>Hipposcarus longiceps</i> (Val.) Southern GBR, New Guinea (5) (7)	<i>Hipposcarus longiceps</i> (Val.)
<i>Scarus longipinnis</i> Randall & Choat Southern GBR (5)	<i>Scarus longipinnis</i> Randall & Choat
<i>Scarus lunula</i> (Snyder) Heron Is., Lord Howe Is. (6) (8)	<i>Scarus chameleon</i> n.sp.
<i>Scarus microrhinos</i> Bleeker Heron Is. (2)	<i>Scarus gibbus</i> Rüppell
<i>Callyodon microrhinos</i> (Bleeker) GBR (3)	
<i>Chlorurus microrhinos</i> (Bleeker) New Guinea (7)	
<i>Bolbometopon muricatus</i> (Val.) New Guinea (7)	<i>Bolbometopon muricatum</i> (Val.)
<i>Callyodon mutabilis</i> Gray GBR (4)	<i>Scarus schlegeli</i> Bleeker?
<i>Callyodon niger</i> (Forsskal) New Guinea (7)	<i>Scarus niger</i> Forsskal
<i>Scarus niger</i> Forsskal Southern GBR (5) (6)	
<i>Pseudoscarus oktodon</i> Bleeker NSW? (1)	Unidentifiable
<i>Xanothron oktodon</i> (Bleeker) New Guinea (7)	<i>Scarus psittacus</i> Rüppell?
<i>Callyodon oviceps</i> (Val.) New Guinea (7)	<i>Scarus oviceps</i> Val.
<i>Scarus oviceps</i> Val. Southern GBR (5) (6)	
<i>Scarus psittacus</i> Forsskal Southern GBR (5)	<i>Scarus psittacus</i> Forsskal
<i>Callyodon pulchellus</i> (Rüppell) GBR (4)	<i>Cetoscarus bicolor</i> (Rüppell)
<i>Cetoscarus pulchellus</i> (Rüppell) New Guinea (7)	
<i>Scarus rivulatus</i> Val. Southern GBR (5)	<i>Scarus rivulatus</i> Val.
<i>Scarops rubroviolaceus</i> (Bleeker) New Guinea (7)	<i>Scarus rubroviolaceus</i> Bleeker
<i>Scarus rubroviolaceus</i> Bleeker Southern GBR (5) (6)	
<i>Scarus scaber</i> Val. Heron Is. (6)	<i>Scarus dimidiatus</i> Bleeker
<i>Scarus schlegeli</i> Bleeker Southern GBR (5)	<i>Scarus schlegeli</i> Bleeker
<i>Scarus schultzi</i> (Smith) Heron Is. (6)	<i>Hipposcarus longiceps</i> (Val.)
<i>Scarus sexvittatus</i> Rüppell Heron Is., Lord Howe Is. (6) (8)	<i>Scarus frenatus</i> Lacepède
<i>Scarus sordidus</i> Forsskal Heron Is., Lord Howe Is. (2) (5) (6) (8)	<i>Scarus sordidus</i> Forsskal
<i>Callyodon sordidus</i> (Forsskal) GBR (3)	
<i>Xanothron sordidus</i> (Forsskal) New Guinea (7)	
<i>Scarus</i> sp. 1 Southern GBR (5)	<i>Scarus chameleon</i> n.sp.
<i>Scarus</i> sp. Lord Howe Is. (8)	<i>Scarus longipinnis</i> Randall & Choat
<i>Cryptotomus spinidens</i> (Quoy & Gaimard) GBR (3) (4)	<i>Calotomus carolinus</i> (Val.) (Quoy & Gaimard)
<i>Calotomus spinidens</i> Heron Is., New Guinea (6) (7)	
<i>Scarus spinus</i> Kner Southern GBR (5)	<i>Scarus spinus</i> Kner

Scarid Identity and Checklist Record

Present Identification

<i>Chlorurus strongylocephalus</i> (Bleeker)	<i>Scarus gibbus</i>
New Guinea (7)	Rüppell?
<i>Scarus tricolor</i> Bleeker	<i>Scarus forsteni</i>
Southern GBR (5)	Bleeker
<i>Scarus venosus</i> Val.	<i>Scarus schlegeli</i>
Heron Is. (6)	Bleeker
<i>Xanothus venosus</i> (Val.)	
New Guinea (7)	
<i>Leptoscarus vaigiensis</i> (Quoy & Gaimard)	<i>Leptoscarus vaigiensis</i>
Moreton Bay, New Guinea, Lord Howe Is. (3) (4) (7) (8)	(Quoy & Gaimard)
<i>Scarus vermiculatus</i> Fowler & Bean	<i>Scarus frenatus</i>
Heron Is. (2)	Lacepède

Zoogeography and Distribution

The distribution of parrotfishes is linked closely to that of coral reefs. Very few species extend beyond this habitat. Indo-Pacific parrotfish faunas exist in three major groupings; the Red Sea, Indian Ocean, and the western and central Pacific. Numbers of species decline across the central Pacific to its eastern boundary. The tropical eastern Pacific has a very depauperate fauna comprising only six species, three of which are unique to the area. There also appears to be a small southern Pacific element. The greatest number of parrotfishes have been recorded from the Indonesian and Philippine archipelagos and the adjacent western Pacific region.

Each of these faunal areas contain mixtures of both area-specific and wide-ranging species. There are a number of species complexes. These closely related species tend to form a geographical series, replacing each other through the major faunal areas. In many instances there is little spatial overlap amongst the species. The geographic distribution of members of the *Scarus schlegeli* (Fig. 2) complex is a good example. These patterns serve as models for reviewing taxonomic problems involving closely related species. In contrast, the wide-ranging species exemplified by *S. ghobban* may have extensive distributions extending from the Red Sea to the eastern Pacific.

The scarid fauna of the Great Barrier Reef, comprising 27 recorded species, is a mixture of three

faunal elements (Table 6). Of the 27 species, 13 are wide-ranging with many of them extending from the Red Sea to the central Pacific. These include *S. sordidus*, *S. rubroviolaceus* and *S. ghobban*. Twelve are characteristic of the Indo-West Pacific region and include *S. rivulatus*, *H. longiceps* and *S. spinus*. Many of these species extend to the northern tropical Pacific. Recent collecting in the southern Pacific has revealed a small but distinctive fauna with a predominantly southern distribution. We include two species here, the recently described *S. longipinnis* and *S. schlegeli*. *Scarus schlegeli* occurs on the Great Barrier Reef and southern Pacific reefs as a distinctive colour variant (Fig. 2).

It is highly probable that with increasing observations on the far northern reefs other species will be added to the Great Barrier Reef list. Species such as *Scarus quoyi*, which occurs in New Guinea, are obvious candidates. Both *S. pyrrhurus* and *S. frontalis* were only sighted very recently on the northern Great Barrier Reef. In addition, there is an unconfirmed sighting of what may be *Scarus oedema*, a species which has previously been recorded from Western Australia but not the Great Barrier Reef.

The Western Australian fauna shares a number of species with the Great Barrier Reef but also contains some distinctive Indian Ocean and western Pacific species. This area requires further collecting, especially on the reefs of the North-West Shelf.

The Australia-wide distribution patterns of the 27 recorded Great Barrier Reef species are shown in Fig. 3.

Table 6. Geographic affinities of scarids recorded from the Great Barrier Reef.

A) Widely distributed species. (West Indian and Pacific Oceans)		B) Western and Central Pacific Species	
<i>B. muricatum</i>	<i>S. ghobban</i>	<i>H. longiceps</i>	<i>S. flavipectoralis</i>
<i>C. bicolor</i>	<i>S. sordidus</i>	<i>S. chameleon</i>	<i>S. forsteni</i>
<i>C. carolinus</i>	<i>S. frenatus</i>	<i>S. pyrrhurus</i>	<i>S. altipinnis</i>
<i>C. spinidens</i>	<i>S. niger</i>	<i>S. frontalis</i>	<i>S. dimidiatus</i>
<i>L. vaigiensis</i>	<i>S. globiceps</i>	<i>S. bleekeri</i>	<i>S. oviceps</i>
<i>S. psittacus</i>	<i>S. rubroviolaceus</i>	<i>S. spinus</i>	<i>S. rivulatus</i>
<i>S. gibbus</i>			
C) Southern Pacific species.			
	<i>S. longipinnis</i>		
	<i>S. schlegeli</i> (southern variant)		

Thirteen of these 27 species extend into northern and western tropical areas. Four of these also extend beyond the limits of reef growth into the edge of temperate areas. These include *S.ghobban*, *S.sordidus* and *L.vaigiensis*, all species with wide geographic distributions. In addition, a number of species may recruit some distance to the south of coral reef environments but do not survive. Observations and records from southern New South Wales include newly recruited *S.rubroviolaceus* and *S.chameleon*.

Latitudinal trends within the Great Barrier Reef region. There is little variation in the number and identity of scarid species from the far northern reefs to those of the Capricorn-Bunker group. The only striking latitudinal change is the absence of *B.muricatum* from the southern reefs. Some relatively rare species which

have Indo-Pacific area affinities are more likely to be encountered on the northern reefs. These include *S.dimidiatus*, *S.pyrrhurus* and *S.frontalis*. Some common species also show latitudinal trends in abundance. *Scarus ghobban* and *S.rivulatus*, which often penetrate coastal waters, tend to be commoner in the south on outer reefs of the Capricorn Bunker group for example, than on the northern reefs. In a survey of 44 reefs from Townsville to Lizard Island, *S.rivulatus* was found to be present on the outer reefs in the Townsville to Cairns section but absent from the far northern outer reefs of the survey area (A.M. Ayling, unpublished). Species with southern Pacific affinities, such as *S.longipinnis*, are commoner in shallow waters in southern reefs than on northern reefs of the continental shelf.

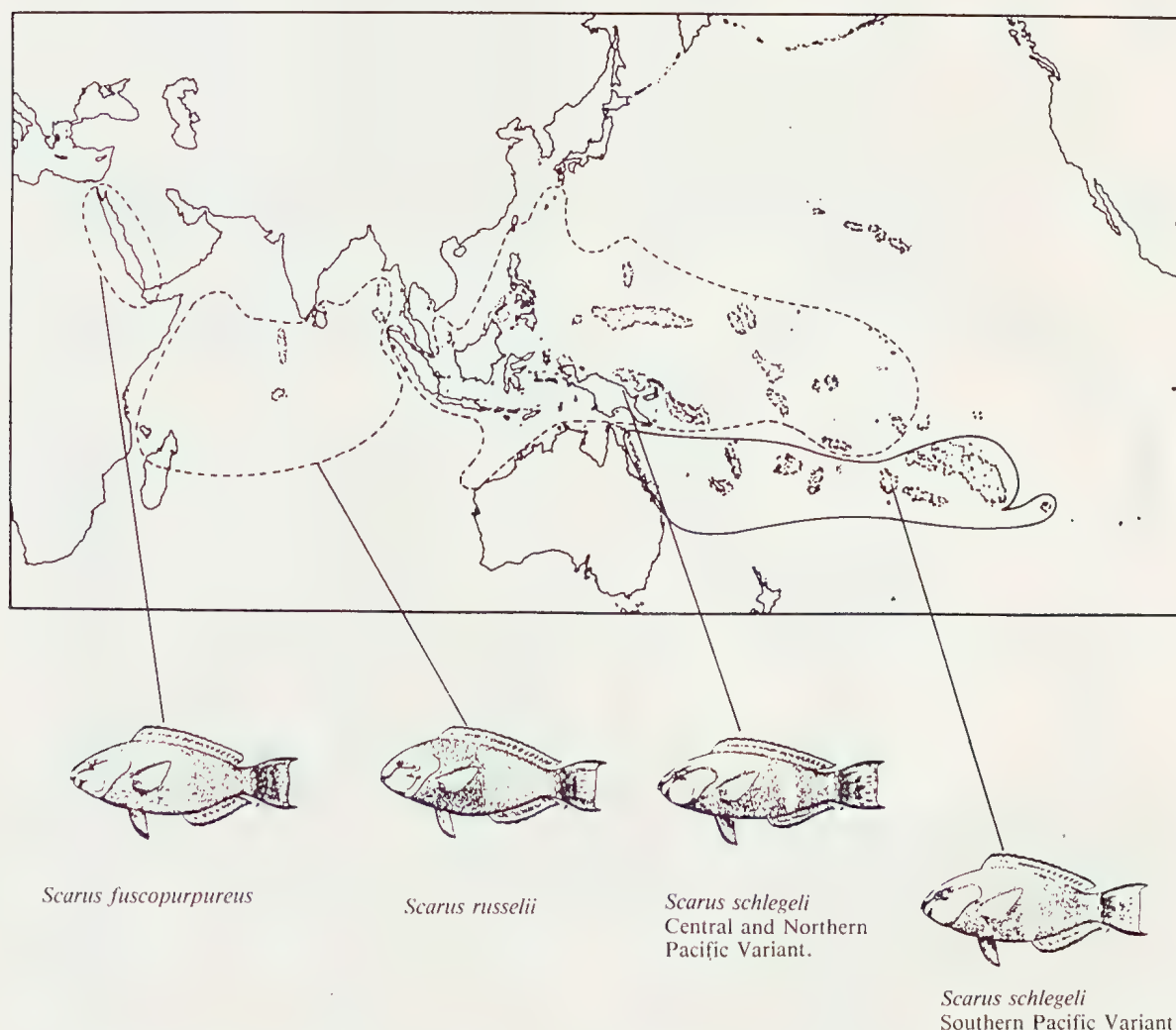


Fig. 2. The distribution of major faunal groupings of scarids within the tropical area extending from the Red Sea to the central Pacific. The faunal areas are exemplified by the geographic distribution of species of the *Scarus schlegeli* complex. *Scarus fuscopurpureus* (Red Sea); *Scarus russelii* (Western Indian Ocean); *Scarus schlegeli* (Central and Northern Pacific variant); *Scarus schlegeli* (Southern Pacific variant). A number of species of scarids have distributions extending over this entire area.

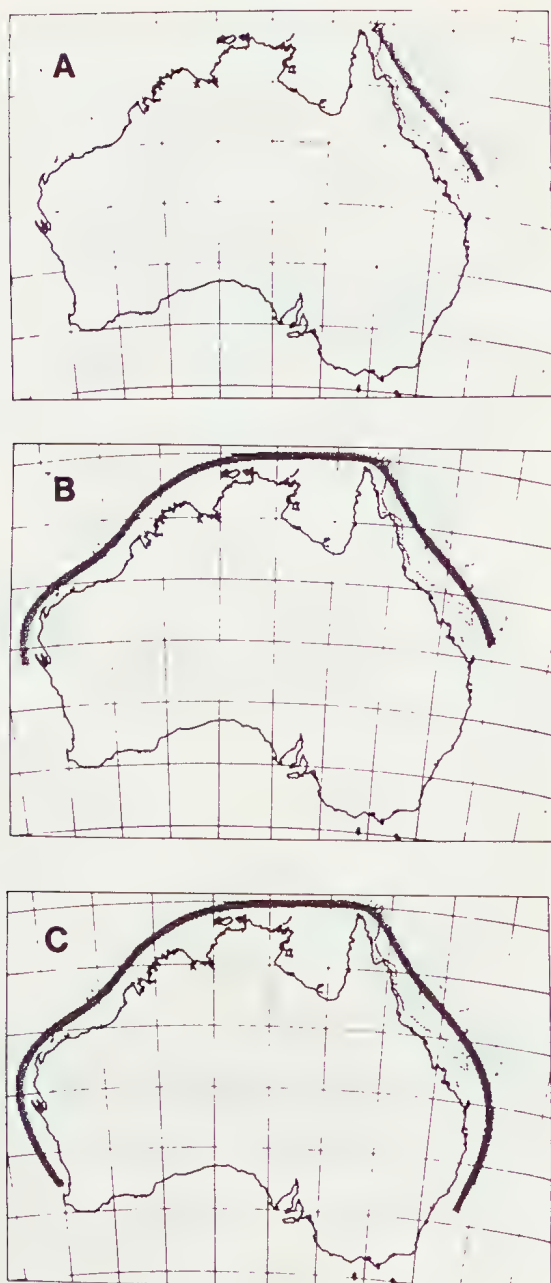


Fig.3. Distribution patterns within Australian waters of the 27 species of scarids recorded from the Great Barrier Reef region.

Category A. Those species recorded from the Great Barrier Reef region only. *C.carolinus*; *C.spinidens*; *B.muricatum*; *C.bicolor*; *H.longiceps*; *S.pyrrhurus*; *S.flavipectoralis*; *S.spinus*; *S.bleekeri*; *S.longipinnis*; *S.frontalis*; *S.altipinnis*; *S.forsteni*; *S.dimidiatus*.

Category B. Those species recorded from northern and western tropical waters. *S.rubroviolaceus*; *S.gibbus*; *S.psittacus*; *S.schlegeli*; *S.chameleon*; *S.globiceps*; *S.oviceps*; *S.frenatus*; *S.niger*. Western Australian waters harbour an additional species *Scarus oedema* which has not been recorded from the Great Barrier Reef.

Category C. Species which are recorded from tropical waters and extend into temperate reefs on the eastern and western coasts: *L.vaigiensis* (not recorded from reef environments of the Great Barrier Reef); *S.sordidus*; *S.rivulatus*; *S.ghobban*.

Longitudinal trends within the Great Barrier Reef region. There are marked cross-shelf trends in scarid abundances and species composition. These trends are associated with the changes in water character, sediment load and reef structure as one follows the environmental gradient from mainland coastal areas to the coral sea (Fig.4).

A number of recent studies (Williams, 1982; Williams & Hatcher, 1983; Russ, 1984a) have provided quantitative information on scarid distribution and abundance. These studies indicate that the number of species, of individuals, and biomass of scarids is significantly lower on inshore reefs when compared to mid- and outer-shelf reefs. Inshore reefs are dominated by *S.rivulatus*, with *S.ghobban* and *S.sordidus* also present but generally rare. The former two species extend to the mid-shelf reefs but are absent or rare on outer reefs. *Scarus sordidus* is a ubiquitous scarid abundant in most areas from which it is recorded. Mid-shelf reefs support slightly greater numbers of species and individuals of scarids than outer-shelf reefs.

A number of surveys by A.M. Ayling and the senior author have provided further data on scarid abundance and distribution patterns which confirm these trends. The information in Table 7 is a compilation of the various recent surveys. The categories indicating abundance are approximations based on a variety of visual survey methods. For details readers are referred to Williams (1982), Russ (1984a) and Choat & Bellwood (1985). An interesting additional point is that the mean size of some species appears to be smaller on outer than on mid-shelf reefs. This trend is apparent on the northern reefs with species such as *S.frenatus* and *C.bicolor*.

Recent information provided by D. Williams and A.M. Ayling identifies an interesting scarid fauna on the reefs of the Coral Sea. Three localities (Flinders Reefs, Herald Cay and Lihou Reef) were examined by various types of visual count techniques. In nearly all localities examined and for all sample techniques used there was an unexpectedly high abundance of the recently described *S.longipinnis*. Other species well represented were *S.sordidus*, *H.longiceps*, *S.altipinnis*, *S.niger*, *C.bicolor* and *S.gibbus*. The Coral Sea scarid fauna has slightly fewer species and for most, a reduced abundance when compared to the shelf reefs. A few species showed a ubiquitous distribution being equally abundant on mid-shelf, outer-shelf and Coral Sea reefs. These include *C.bicolor*, *S.rubroviolaceus*, *S.sordidus*, *S.gibbus* and *S.niger*, species which have broad geographic distributions. Only two species, *S.sordidus* and *S.gibbus*, extended from inshore reefs to the Coral Sea. A summary of longitudinal trends in distribution is provided in Table 7.

Most scarid species also have characteristic habitat associations within reef systems. These are summarised under each species description.

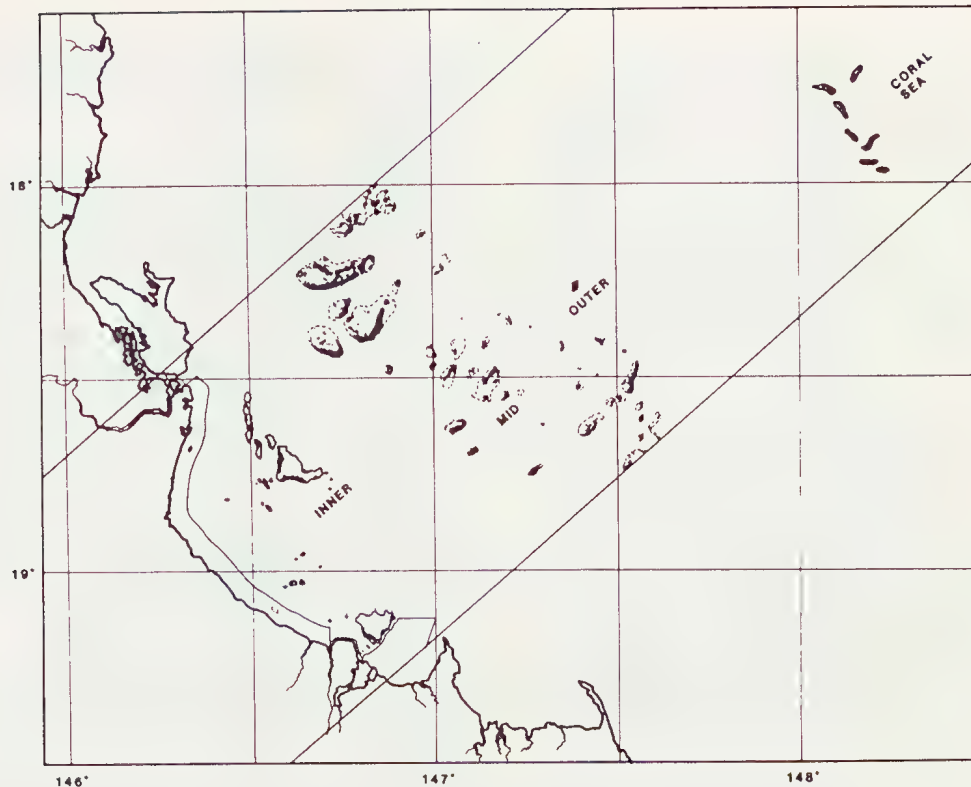


Fig. 4. The geographic distribution of reef sampling areas in the central region of the Great Barrier Reef. Inner, Mid and Outer groups of reefs are located on the continental shelf. The remaining reef group is in the Coral Sea proper. Abundances and species composition of scarid faunas on these reef groupings were used to determine longitudinal trends.

Table 7. The cross-shelf distribution of Great Barrier Reef scarids. Species placed in abundance categories. (See text for details)

Species	Cross Shelf Reef Position			
	Inner	Mid	Outer	Coral Sea
<i>L.vaigiensis</i>	—	—	—	—
<i>C.spinidens</i>	—	—	—	—
<i>S.gobban</i>	rare	rare	—	—
<i>S.rivulatus</i>	moderate	moderate	rare	—
<i>S.globiceps</i>	rare	moderate	moderate	—
<i>S.gibbus</i>	rare	common	common	rare
<i>S.sordidus</i>	rare	common	common	common
<i>C.carolinus</i>	—	rare	rare	rare
<i>C.bicolor</i>	—	rare	moderate	moderate
<i>H.longiceps</i>	—	rare	moderate	moderate
<i>S.rubroviolaceus</i>	—	rare	rare	rare
<i>S.altipinnis</i>	—	moderate	moderate	moderate
<i>S.spinus</i>	—	moderate	rare	rare
<i>S.chameleon</i>	—	moderate	moderate	moderate
<i>S.schlegeli</i>	—	moderate	moderate	rare
<i>S.psittacus</i>	—	moderate	rare	rare
<i>S.niger</i>	—	common	moderate	moderate
<i>S.frenatus</i>	—	moderate	moderate	rare
<i>S.forsteni</i>	—	rare	rare	rare
<i>S.dimidiatus</i>	—	rare	rare	rare
<i>S.oviceps</i>	—	rare	rare	rare
<i>S.frontalis</i>	—	rare	rare	rare
<i>S.longipinnis</i>	—	rare	rare	common
<i>B.muricatum</i>	—	rare	moderate	rare
<i>S.flavipectoralis</i>	—	moderate	rare	—
<i>S.pyrrhurus</i>	—	rare	rare	—
<i>S.bleekeri</i>	—	rare	rare	—

Colour Phases and Reproductive Biology

There are usually three distinct colour phases in scarids: juvenile phase, initial phase (IP) (subadults, females and some types of male), and terminal phase (TP) (characteristic of large males). These terms were adopted at the International Symposium on Intersexuality in the Animal Kingdom in Mainz, July 1974. Further details of definition are provided by Warner & Robertson, 1978. The abbreviations IP and TP will be used to designate initial and terminal phase throughout this study. The juvenile phase as seen in newly recruited individuals will be dealt with in a forthcoming publication (Bellwood & Choat, in prep.). In general, IP fish display muted colour patterns characterized by brown, grey, reddish or yellow hues. There are usually few distinguishing markings and, to the non-specialist worker, most species of scarids appear to be very similar when in the IP. TP fish are brightly coloured with greens predominating. Most species display highly characteristic markings around the head and snout. Scarids in terminal phase colouration are usually easy to identify. In some areas, however, complexes of closely related species co-occur, so caution is required. The major problem confronting the student of scarid taxonomy is the reliable separation of scarids with IP colouration. Finally, the colour patterns of most scarids both in IP and TP may vary in response to behavioural characteristics. Interactions between species or within species during reproductive behaviour often result in rapid and striking modifications to the basic colour pattern. These are difficult to photograph. Paintings and diagrams recording the variation to colour patterns associated with short term responses in an exemplary species (*S. rivulatus*) are reproduced in Plate 11, F–J. Careful observation of live scarids is required to obtain a comprehensive understanding of the range of variation possible.

Of the 27 species of parrotfishes dealt with here, 23 are dichromatic with distinct IP and TP colours. Three, *Bolbometopon muricatum*, *Scarus frontalis* and *Scarus niger*, appear to be monochromatic in Australian waters. One species, *Scarus gibbus*, does not display the usual size-associated distribution of colour phases.

The sequence of colour changes seen in adult parrotfishes is intimately linked to patterns of sexual ontogeny. Scarids are generally protogynous hermaphrodites (Choat & Robertson, 1975; Robertson & Warner, 1978; Randall & Bruce, 1983) with most females eventually assuming male identity by a process of sexual inversion. This process produces secondary males. In many species there is a varying proportion of primary males which maintain male sexual identity from birth. Females and smaller primary males display the IP colour. Larger males display the TP colour; these may be of either secondary or primary derivation. Females may assume secondary male identity and TP colour by synchronous sex and colour change. Primary males with IP colour may simply undergo colour change to achieve the terminal phase. Species with both primary

and secondary males in their breeding populations are described as diandric; those with secondary males only as monandric.

Although the sequences of colour patterns and sexual ontogeny in scarid fishes are well described, the behavioural and ecological consequences of different patterns of sex and colour change are not. Previous studies (Choat & Robertson, 1975; Randall & Choat, 1980) of Great Barrier Reef scarids have suggested the following general classification of scarid reproductive patterns. Some species are strongly diandric (*S. globiceps*, *S. rivulatus*, *S. psittacus*) with a relatively high proportion of primary males. These usually have high population densities, form schools, and display local spawning migrations to specific sites. Here, both group spawning involving IP males and females, and pair spawning involving a terminal male and a single female occur. Group spawnings appeared to involve large numbers of IP males; TP males at spawning sites were highly antagonistic to IP males.

Weakly diandric and monandric species (*S. niger*, *S. frenatus*) were seen as site-attached scarids in which a single terminal male spawned consistently with a small harem of females in the pair spawning mode. Two species were considered to characterize the different ends of this reproductive spectrum: *Scarus globiceps* as a strongly diandric species with consistent group spawning episodes, and *S. niger* as a strongly site-attached monandric species with a harem, pair spawning mode. However, the small numbers of mature males in the IP found in site-associated species, such as *S. frenatus*, were always a problem for such a classification. As such males were apparently associated with movements of large numbers to particular sites it was difficult to visualize their role in weakly diandric species.

Recent observations on the northern reefs of the Great Barrier Reef indicate that the above generalizations are too simplistic. Most scarids, including members of apparently site-attached species such as *S. niger* and *S. frenatus*, will undergo local spawning migrations to specific sites. Observations at Lizard Island have demonstrated that spawning behaviour is more variable than previously indicated. Group spawning at migratory sites involving very small numbers of IP males (4–5 individuals) was observed to occur in weakly diandric species such as *S. schlegeli*. IP males in such circumstances displayed highly characteristic changes in colour pattern during reproductive behaviour. Pair spawning was observed in *S. niger* and *S. frenatus* involving large males and single females from a waiting pool of females which had apparently migrated to spawning sites. In strongly diandric species, such as *S. rivulatus*, a number of episodes were observed of mixed group spawning involving small numbers of IP males, a single TP male and a single female. There were no aggressive interactions amongst males prior to the spawning run. Such observations indicate highly variable reproductive behaviour in scarids. Details of reproduction and sexual status are included under the individual species headings.

Key to Species of Scaridae from the Great Barrier Reef Region
(Key refers to adult individuals)

1. Horizontal rows of scales on cheek 1; pectoral rays 13 (rarely 12 or 14); gill rakers 8–14; jaws opposing or upper jaw enclosed by lower when mouth closed. 2
 - Horizontal rows of scales on cheek 2–3; pectoral rays 13–17 (rarely 13 or 17); gill rakers 16–81; lower jaw enclosed by upper when mouth closed. 4
2. Teeth in jaws fused to form dental plates; upper jaw enclosed by lower when mouth closed; membranes of spinous portion of dorsal fin incised $\frac{1}{4}$ to $\frac{1}{3}$ length of spines. *Leptoscarus vaigiensis*
 - Teeth in jaws not fused but incisiform, overlying bony ridge of jaws; jaws opposing when mouth closed; membranes of spinous portion of dorsal fin slightly emarginate between spines. 3
3. Incisiform teeth of upper jaw in 3–6 oblique imbricate rows; body depth 2.2–2.75 in SL; gill rakers 10–14; caudal fin rounded in young, becoming truncate to emarginate in adults; a posterior whitish margin on caudal fin. *Calotomus carolinus*
 - Incisiform teeth of upper jaw in a single row; body depth 2.5–3.2 in SL; gill rakers 8–10; caudal fin rounded at all stages; no posterior white margin on caudal fin. *Calotomus spinidens*
4. Outer surface of dental plates granular with individual teeth visible on dental plates; no canine teeth on dental plates; posterior nostril notably larger than anterior (up to 4 times larger), oval or slit-like; gill rakers 16–24; each upper pharyngeal bone with 3 rows of molariform teeth, those of the lateral row rudimentary, inner rows of teeth not interdigitating. 5
 - Outer surface of dental plates relatively smooth; canine teeth often present posteriorly on side of dental plates; posterior nostril not notably larger than anterior (except *S. ghobban*); gill rakers 38–81; each upper pharyngeal bone with 1 row of large molariform teeth, with or without a rudimentary lateral row, inner rows of teeth interdigitating. 6
5. Dorsal profile of head with a hump anterodorsal to eye (evident on specimens at least as small as 200 mm SL); body deep, the depth 2.1–2.5 in SL; profile of snout steep, nearly vertical in large adults; individual teeth with small raised tubercles; median predorsal scales 2–5 (usually 4); one row of scales on interopercle; pectoral rays 15 or 16; gill rakers 16–18; adults dull green to blue-green (not sexually dichromatic). *Bolbometopon muricatum*
 - Dorsal profile of head slightly and evenly convex; body depth 2.5–2.8 in SL; profile of snout sloping; median predorsal scales 5–7; two rows of scales on interopercle; pectoral rays 14 or 15 (usually 14); gill rakers 20–24; IP reddish, yellow on back, the scales on side of body edged and spotted with black; terminal male green, head and anterior body with orange spots, scales edged with orange. *Cetoscarus bicolor*
6. Dental plates narrow, their height about 1.5–2.0 in orbit diameter; head pointed, with a distinctly angular snout; eye near dorsal profile, the interorbital space slightly convex; cheek scales small, in a nearly isolated patch; caudal fin double emarginate. *Hipposcarus longiceps*
 - Dental plates not narrow, their height usually greater than orbit diameter; head not pointed; eye not near dorsal profile, the interorbital space strongly convex; cheek scales not small and not in an isolated patch; caudal fin rounded to lunate. 7
7. Dorsal profile of head rising steeply from mouth to level of eye, then curving abruptly to nearly straight for remaining profile of head; rudimentary lateral row of teeth on upper pharyngeal bones may be present in small juveniles

- but lost in larger individuals; median predorsal scales 6–7; IP reddish except yellowish grey side of body; body scales with narrow blackish edges and short blackish markings, fins red; terminal male green dorsally, shading to yellowish on sides and light blue–green ventrally; upper lip narrowly salmon with a broad blue–green band above; lower lip broadly blue–green at margin; chin salmon crossed by a blue–green band which joins that of lip and passes to below orbit. *Scarus rubroviolaceus*
- Snout not shaped as above (large *S.gibbus*) and *S.frontalis* have steep snout profiles but the angular break in contour is above eye level); a row of rudimentary teeth laterally on each upper pharyngeal bone nearly always present; colour not as above. 8
8. Pectoral rays usually 16 (rarely 15 or 17); cheek scales in 3 rows, usually with 5–7 scales in third (lower) row; dorsal profile of small individuals strongly convex, of large individuals very steep from mouth to above level of eye, then curving to slightly convex for remainder of profile; 2 colour phases: one green to blue–green with a narrow salmon pink bar on each scale of body (except ventrally); ventral part of head pale with an irregular bright blue–green band from corner of mouth across cheek to operculum; a red phase with body uniform reddish becoming yellowish ventrally. *Scarus gibbus*
- Pectoral rays 13–16 (rarely 16); cheek scales in 2 or 3 rows, (when 3, the third row with no more than 4 scales, except for *S.forsteni* and *S.niger*); dorsal profile of head not as above; colour not as above. 9
9. Median predorsal scales usually 4; scale rows on cheek 2 or 3. 10
- Median predorsal scales usually 5–7; scale rows cheek 3. 19
10. Pectoral rays usually 14; lips cover half or more of dental plates; scale rows on cheek 2 or 3. 11
- Pectoral rays usually 15; lips cover less than half of dental plates; scale rows on cheek 2. 16
11. Scale rows on cheek 2. 12
- Scale rows on cheek 3, the lowermost row with 1–3 scales. 13
12. Caudal fin of IP slightly emarginate; IP brown to reddish brown with a large dark brown spot anterobasally on first interspinous membrane of dorsal fin and a narrow whitish posterior margin on caudal fin; terminal male with 3 blue–green bands extending posteriorly from eye, the lowermost passing forward submarginally onto upper lip; head above this band lavender grey. *Scarus psittacus*
- Caudal fin of IP slightly rounded; IP purplish to olivaceous brown, edges of scales orangish, with 5 curved pale bars on body; terminal male dark green, sometimes suffused with purple, edges of scales orange–red to salmon; a squarish spot of bright yellow on back at level of eleventh to thirteenth vertical scale rows of body and below first dorsal ray. *Scarus schlegeli*
13. Dorsal spines and rays long, the longest spine 1.7–2.1 in head; pelvic fins long, 1.15–1.5 in head; a broad blue–green bar from in front of eye to chin, another across interorbital space, and a third prominent bar across cheek from lower edge of eye to pectoral base. *Scarus longipinnis*
- Dorsal spines and rays not long, the longest spine 2.2–3.2 in head; pelvic fins not long, 1.6–2.1 in head; colour not as above. 14
14. No overlapping lateral pair of small scales anterior to median predorsal scales; IP grey, caudal fin dark purplish, pectoral fins with large yellow spot at base; terminal male with head and anterior third of body brown with a broad green band from front of snout through lower part of eye to end of opercle, posterior $\frac{2}{3}$ of body abruptly blue–green with narrow orange bar on each scale. *Scarus flavipectoralis*

- Transverse overlapping pair of scales directly anterior to first median predorsal scale; colour not as above. 15
15. Body depth 2.3–2.6 in SL; head bluntly rounded anteriorly, dorsal and ventral profiles almost identical; IP dark brown with four or five indistinct pale bars on body (from pale centers of scales) or may be uniform blackish brown; terminal male with head blue–green to green, shading to yellow on operculum, with two broad curved transverse salmon bands on chin. *Scarus spinus*
- Body depth 2.5–2.8 in SL; head somewhat pointed anteriorly; dorsal profile of head smoothly convex (or with only a slight angularity above eye in large males); IP pale greyish to brown with yellowish caudal fin; TP with single green band across interorbital space. *Scarus chameleon* n.sp.
16. IP uniform dark brown, caudal fin red with a narrow black posterior margin; terminal male with body purplish anteriorly, greenish yellow angular patch in middle, and blue–green posteriorly, each scale with an orange mark (narrow vertical bar anteriorly and round spot posteriorly). *Scarus pyrrhurus*
- Colour not as above. 17
17. Snout of terminal males with very steep profile to above level of eye where there is an abrupt angle, rest of profile to origin of dorsal fin nearly straight; both initial and terminal phases green with pink or purplish bar on each scale of body, head with irregular reddish to pink markings around eye (except ventrally), on chin and corner of mouth. *Scarus frontalis*
- Dorsal profile of head of terminal males smoothly convex; colour not as above (IP brown); head of terminal male phase without irregular reddish to pink markings. 18
18. Initial phase dark brown, edges of scales orangish, body with five faint yellowish bars, shading ventrally to dull orange–red and posteriorly to yellowish, caudal fin and peduncle yellowish; terminal male with large whitish area on cheek bordered with blue–green; dental plates of both phases white. *Scarus bleekeri*
- IP brown, sometimes with two rows of small whitish spots on side, becoming red around mouth (a transient colour phase displays broad whitish bar on caudal peduncle containing a large dark brown spot at caudal fin base); terminal male green, the broad central region of body mainly yellow, becoming green ventrally, caudal peduncle distinctly lighter green; dental plates of IP reddish white, of terminal male green. *Scarus sordidus*
19. Pectoral rays usually 15. 20
- Pectoral rays usually 14. 21
20. Spinous portion of dorsal fin and elongate first soft ray distinctly higher than rest of soft portion of fin; caudal fin of adults double emarginate (broadly rounded in center, the lobes produced); IP brownish red, often with series of small whitish spots along side of body; head of terminal male orange, shading posteriorly to green, with broad blue–green transverse bands on snout and chin, and dark blue–green spots and irregular markings around eye and postorbitally; dental plates of both phases dark blue–green. *Scarus altipinnis*
- Spinous portion of dorsal fin not higher than soft portion; lobes of caudal fin of TP male extended but not double emarginate; IP phase yellow, centers of scales blue, often with five blue bars on body; terminal male light green, scales edged with salmon pink; light blue–green horizontal bands through upper and lower edges of eye and one extending posteriorly from middle of orbit, intervening bands pale salmon; posterior nostril 2–5 times larger than anterior. *Scarus ghobban*
21. Caudal fin of IP slightly rounded, of terminal male truncate; IP yellowish, shading to white ventrally, with 5 slightly diagonal grey–brown bars on upper

half of body which are broader than yellow interspaces; terminal male solid blue-green on upper head posterior to mid-interorbital space and anterodorsal body, rest of body blue-green with orange edges on scales; diagonal purplish brown band runs from eye to end of opercular membrane with, below and adjacent, pale salmon band edged in blue-green, continuing below eye as blue-green band which expands broadly onto chin and front of snout (except narrow edge of upper lip which is salmon pink).

- *Scarus dimidiatus*
- Caudal fin of IP truncate to emarginate, of terminal male emarginate to double emarginate or lunate; colour not as above. 22
22. No canine teeth on dental plates; IP with upper half of head and body dark grey, lower half pale yellowish to pinkish (though scales may be edged in grey), with diagonal yellow bar on back beginning above pectoral fin tip (second fainter yellow bar may be present posterior and parallel to first); terminal male with head above level of lower edge of eye and anterodorsal part of body to base of eighth dorsal spine dark purplish, rest of head and body abruptly blue-green, scales of body edged in salmon pink to orange; dental plates of IP white, of terminal male dark blue-green. *Scarus oviceps*
- Canine teeth usually present posteriorly on side of dental plates, at least on upper plate of large males; colour not as above. 23
23. Median predorsal scales usually 7. 24
- Median predorsal scales usually 5 or 6. 25
24. Penultimate anal ray prolonged in large males, its length 1.5–1.6 in head; small individuals greenish brown on body with small black spots; head orangish brown, becoming orange-red anteriorly, with green markings (notable are two bands on chin and one at base of upper lip and small black-edged green spot behind upper end of gill opening); large individuals similar in colour but dark spots on body faint or absent and overall colour more purplish; dental plates blue-green. *Scarus niger*
- Penultimate anal ray of terminal male not prolonged; IP reddish brown, becoming grey over side of body with 5–7 dark brown stripes, fins red; terminal male green on lower half of head and body, posterior to a vertical at base of fifth dorsal soft ray; rest of head and body green with numerous small orange spots and short irregular lines; dental plates of IP white, of terminal male blue-green. *Scarus frenatus*
25. Caudal fin of IP emarginate, of terminal male lunate; 3 rows of cheek scales with 4–5 in ventral row; IP olivaceous to light reddish brown with broad longitudinal blue band along side of body, a white spot frequently present in life on side near tip of pectoral fin, and caudal fin orange-red; terminal male green, scales of body edged in salmon (green pale on lower side, hence salmon predominating); lips edged in salmon pink (the upper more broadly), both with wide submarginal blue-green band; pectoral fins blue-green with median streak of purplish orange; dental plates of IP white, of terminal male blue-green. *Scarus forsteni*
- Caudal fin not lunate; colour not as above. 26
26. Caudal fin of IP truncate, of terminal male slightly to moderately emarginate; 3 rows of cheek scales with 2–3 in ventral row; IP brown to brownish grey with 2 or 3 whitish stripes on abdomen; terminal male green with an orange bar on each scale except abdomen where green is arranged in 3 stripes, and anterodorsally where green is broken into small spots; salmon pink stripe edged in blue-green passing from front of snout through eye, and blue-green lines radiating dorsally from orbit; blackish spot at or near base of fourth dorsal spine. *Scarus globiceps*
- Caudal fin rounded in IP, truncate in TP; 3 rows cheek scales with 1–2 scales

in ventral row; IP grey to reddish brown with 2 to 3 whitish stripes on abdomen (in life light greyish with a distinct yellowish caste); lower head of terminal male orange with irregular blue-green lines and small spots on snout, chin, cheek and radiating from eye. *Scarus rivulatus*

Calotomus carolinus (Valenciennes)

Plate 1D, E

Callyodon Carolinus Valenciennes in Cuvier & Valenciennes, 1840: 291 (type locality, Caroline Islands).

Callyodon genistriatus Valenciennes in Cuvier & Valenciennes, 1840: 293 (type locality unknown).

Callyodon sandwicensis Valenciennes in Cuvier & Valenciennes, 1840: 295 (type locality, Hawaiian Islands).

Callyodon brachysoma Bleeker, 1861: 244 (type localities, Ambon and Ternate).

Calotomus xenodon Gilbert, 1890: 70 (type locality, Socorro Island, Revillagigedo Islands).

Calotomus irradians Jenkins, 1900: 58, fig. 15 (type locality, Hawaiian Islands).

Calotomus snyderi Jenkins, 1903: 467, fig. 25 (type locality, Honolulu).

Scarichthys rarotongae Seale, 1906: 59, fig. 8 (type locality, Rarotonga, Cook Islands).

Cryptotomus albimarginatus Fourmanoir & Guézé, 1961: 19, fig. 6 (type locality, Réunion).

Material examined. Two specimens, Heron Island AMS I.15502-001, USNM 235594; one specimen (juvenile), Lizard Island, AMS I.25905-002.

Diagnosis. Teeth not fused to form dental plates; upper jaw with slightly curved, bluntly pointed, incisiform, imbricate teeth in 3–6 oblique rows (number of teeth increasing with size), lower jaw with 4–7 rows; 1 or 2 strongly curved canine teeth on side of upper jaw which flare laterally and posteriorly; pectoral rays 13; single row of 4 or 5 scales on cheek below eye; median predorsal scales 3 or 4 (usually 4); gill rakers 10–14; body depth 2.2–2.75 in SL; head 2.9–3.25 in SL; snout 2.3–3.1 in head; interorbital space slightly convex; dorsal spines flexible; caudal fin slightly rounded in small individuals, truncate to slightly emarginate in large IP fish, and slightly emarginate to deeply emarginate or double emarginate in terminal males, upper caudal lobe usually longer than lower.

Colour pattern. IP: Body greyish to yellowish brown, often faintly blotched with darker brown and flecked with whitish, shading ventrally to reddish or orangish brown; an orangish line often present from orbit to corner of mouth; three reddish lines may extend posteriorly from orbit; fins similar in colour to body but with more pale flecks; dark spot often present centrally on first interspinous membrane of dorsal fin, large dark spot basally on posterior part of fin; a similar but smaller spot posterobasally on anal fin; caudal fin with whitish posterior margin; pectoral fins broadly dark brown basally, shading to pale on about distal two thirds.

TP: Body brownish red, strongly suffused with green or blue-green (green dominating in most individuals), scale edges with narrow vertically elongate bars or spots of salmon pink; head blue-green with narrow salmon pink to orange bands radiating from orbit; one or more short bands of the same colour on front of snout and chin; dorsal and anal fins blue-green with irregular longitudinal bands of salmon pink or orange, the dorsal with a blackish spot on first membrane and sometimes on second; unscaled part of caudal fin blue-green with irregular salmon pink to orange markings and narrow whitish posterior margin; pectoral fins greenish on about basal two thirds with some orangish streaks, becoming pale on outer third.

Remarks. The synonymy and species description follows Bruce & Randall (1985). Most recent authors have erroneously used the name *Calotomus spinidens* for this parrotfish. Gosline & Brock (1960) applied the name *C. sandwicensis* (sic) to the species in the Hawaiian Islands.

Calotomus carolinus ranges from the coast of East Africa (at least as far south as 21°) throughout most of the tropical Indo-Pacific region to Mexico (Bruce & Randall, 1985). It appears to be absent from the Red Sea, Persian Gulf and Easter Island. In the western Pacific it ranges from the Ryukyu Islands to the southern Great Barrier Reef.

Calotomus carolinus is a protogynous hermaphrodite. Robertson et al. (1982) reported on the collection of 22 IP fish (to 253 mm SL) at Aldabra, all of which were females (maturing at a SL of about 160–180 mm) and six TP fish, 240–270 mm SL, all of which were secondary males.

In Australia this species has been consistently misidentified as *C. spinidens* (Table 5). On the Great Barrier Reef *C. carolinus* is usually rare and may be observed in reef crest and reef base habitats on mid- and outer-shelf reefs, occurring in pairs or as individuals. Small IP individuals were observed at Lizard Island and were readily recognizable underwater by the high body profile and the prominent light-coloured eyes. Small numbers were observed at Herald Cay and Lihou Reefs in the Coral Sea by A.M. Ayling. This species has not been recorded from Western Australia. Pair spawning was observed once at Lizard Island. The terminal phase male was approximately 300 mm SL and displayed a prominent white blotch on the side during spawning. Two specimens collected at Heron Island were 397 and 273 mm SL. The largest specimen examined by Bruce & Randall (1985) was 398 mm SL (BPBM 16658), from Pitcairn.

Calotomus spinidens (Quoy & Gaimard)

Plate 1C

Scarus spinidens Quoy & Gaimard, 1824: 289 (type locality, Vaigiou = Waigeo).

Callyodon Waigiensis Valenciennes in Cuvier & Valenciennes, 1840: 296 (new name for *Scarus spinidens* Quoy & Gaimard).

Callyodon hypselosoma Bleeker, 1855b: 425 (type locality, Ambon).

Callyodon moluccensis Bleeker, 1861: 243 (type localities, Celebes, Ternate, Batjan, Timor, Ambon, Ceram and Banda).

Material examined. One specimen, 5 miles northwest of Lizard Island, AMS I.20752-027.

Diagnosis. Upper jaw with outer row of prominent, protruding, slightly flattened, conical teeth (well spaced on large individuals), last 1 or 2 recurved, this series buttressed behind by a bony ridge which has 1 row of small close-set incisiform teeth (with rounded, not truncate tips) posteriorly; medial to bony ridge one row of well spaced, short, conical teeth, medial to these, two more short conical teeth; lower jaw with about 3 oblique rows of bluntly pointed, incisiform, imbricate teeth anteriorly on external face of bony ridge, series of small, close-set incisiform teeth (with rounded tips) posteriorly; pectoral rays 13 (rarely 12); single row of 4 or 5 scales on cheek below eye; median predorsal scales 4; gill rakers 8-10; body depth 2.5-3.2 in SL; head 2.8-3.2 in SL; snout 2.75-3.5 in head; interorbital space slightly convex; dorsal spines flexible; caudal fin rounded at all sizes.

Colour pattern. IP: body greenish brown, finely and densely flecked with whitish, shading to whitish ventrally, with 3-4 longitudinal rows of whitish spots (often only upper 2 rows visible); faint lateral pale stripe often present on body; median and pelvic fins whitish to yellowish, stippled and blotched with white; anal fin with pink spot basally on each ray; pectoral fins uniformly pale.

TP: males similar in ground colour but have rows of small orange spots on body and basally on dorsal fin, small orange spots or short lines on head, 2 diagonal orange lines from eye to corner of mouth; blackish spot near base of second interspinous membrane of dorsal fin; 2 irregular orange bands in anal fin; blackish bar across pectoral fin base.

Remarks. The synonymy and description follows Bruce & Randall (1985). Schultz (1958) and others have erred in using the name *C. spinidens* for the species identified herein as *C. carolinus*. Schultz placed *Callyodon moluccensis* Bleeker and *C. spinidens* Bleeker in the synonymy of *Calotomus japonicus* (of Bleeker's *C. spinidens*, Schultz wrote, 'not of Quoy & Gaimard', but Bleeker's material is the true *spinidens*). Examination of Schultz' specimens of *C. japonicus* at the USNM revealed that only those from Japan are *C. japonicus*. Most of the rest are the true *C. spinidens*; one lot from the Palau Islands is *Leptoscarus vaigiensis*.

Calotomus spinidens occurs from the coast of Africa

(at least as far south as Delagoa Bay, Mozambique) eastwards to the Marshall Islands in the northern Pacific, and Tonga in the southern Pacific. It is absent from the Persian Gulf, and records from the Red Sea appear to be misidentifications of *C. viridescens* (Ruppell). In the western Pacific it ranges from the Ryukyu Islands and Taiwan south to the Great Barrier Reef (AMS I.20752-027 is a 125 mm male taken 5 miles WNW of Lizard Island). This species appears to be rare in Australian waters.

Robertson et al. (1982) observed 10% functional primary males among the IP fish at Aldabra, and both primary and second males in the terminal phase (but predominately secondary males). Four intersex individuals were found among IP fish. The smallest mature IP males and females were both 67 mm SL. The smallest TP male was 81 mm SL.

This species was not observed underwater on the Great Barrier Reef. It appears to inhabit seagrass beds in deeper water between reefs on the northern and central GBR. The largest specimen examined by Bruce & Randall (1985) was 148 mm SL (USNM 201503), from the Amirante Group of the Seychelles.

Leptoscarus vaigiensis (Quoy & Gaimard)

Plate 1A,B

Scarus vaigiensis Quoy & Gaimard, 1824: 288 (type locality, Vaigiou = Waigeo).

Scarus (Callyodon) caeruleo-punctatus Ruppell, 1835: 24, pl. 7, fig. 2 (type locality, Red Sea).

Scarus rubro-notatus Ehrenberg in Cuvier & Valenciennes, 1840: 212 (type localities, Gulf of Arabia and Red Sea).

Scarus auritus Kuhl and Van Hasselt in Cuvier and Valenciennes, 1840: 218 (type locality, Java).

Scarus naevius Valenciennes in Cuvier & Valenciennes, 1840: 253 (type locality, Seychelles).

Scarus Bottae Valenciennes in Cuvier & Valenciennes, 1840: 262 (type locality, Jeddah, Red Sea).

Calliodon chlorolepsis Richardson, 1840: 137, pl. 64, figs 4-7 (type locality, Hong Kong).

Material examined. One specimen, Rottneest Island, WAM P.26842-001; one specimen, Caloundra, Qld, QM I.5973; two specimens, Moreton Bay, QM I.4705, I.12044; one specimen, Lord Howe Island, AMS I.2789; one specimen, Sydney, AMS IB.4519; one specimen, New Caledonia, AMS IB.2403.

Diagnosis. Teeth fused to form dental plates, upper enclosed by lower when mouth closed; males with 2-7 canine teeth anteriorly near base of upper dental plate; lips covering dental plates; pectoral rays 13 (rarely 12 or 14); single horizontal row of scales on cheek; median predorsal scales usually 4; gill rakers 10-14; body elongate, depth 2.85-3.8 in SL; head length 2.95-3.35 in SL; snout 2.55-2.9 in head; interorbital nearly flat; dorsal spines flexible; membranes of spinous portion of dorsal fin incised $\frac{1}{4}$ - $\frac{1}{3}$ length of spines; caudal fin rounded.

Colour pattern. IP: body olivaceous, spotted and mottled with whitish and dark brown, shading to whitish

or pale yellow ventrally; two irregular transverse whitish bands on chin extending upward to cheek; large brown blotches on dorsal fin, first covering most of first interspinous membrane and part of second; anal fin with alternating diagonal dark brown and whitish bands; dark brown bar on pectoral base; large reddish blotch basally on pelvic fins.

TP: greenish brown, mottled with darker brown and whitish, shading to light brownish or greenish yellow ventrally, with numerous small blue spots on head and body, some short blue lines radiating from eye; irregular whitish stripe from above pectoral base along side of body to slightly below mid-base of caudal fin; opercular membrane often orange-red; fins similar in colour to initial phase but not as strongly marked.

Remarks. The synonymy and species description follows Bruce & Randall (1985). *Leptoscarus vaigiensis* is a wide-ranging species, occurring from the Red Sea and coast of East Africa to Oceania. In the South Pacific it extends to Easter Island, but north of the equator it is known only to the Palau Islands and Mariana Islands. It has not been found in the Caroline Islands, Marshall Islands, Gilbert Islands, Line Islands or the Hawaiian Islands. In the western Pacific it ranges from southern Japan to Queensland; there is one valid record from northern New Zealand (Russell & Ayling, 1976). In Australia the species has an extensive distribution from Sydney Harbour in the east (R. Kuiter, pers. comm) to Rottnest Island in the west. The preferred habitat appears to be algal and seagrass beds. In Australia, *L. vaigiensis* has been recorded from a number of localities (Table 5). It was not observed by the authors in any coral reef environments although it may occur on northern inshore reefs (A.M. Ayling, pers. comm.). The largest specimen examined by Bruce & Randall (1985), 327 mm SL (WAM P.26842-001) was from Rottnest Island. The species does not approach this size in warmer waters.

Robertson et al. (1982) reported that *L. vaigiensis* appears to be gonochoristic, i.e., exhibits no change in sex. No other scarid fish is known in which there is no female to male sex reversal. Mature IP females of *L. vaigiensis* were found as small as 69 mm SL, and IP males as small as 72 mm SL. Males are capable of changing from the initial phase to the terminal phase at a small size (as small as 85 mm SL), but there is a broad overlap in the size of IP and TP males. Females appear to reach about the same maximum length as males. Both pair spawning and group spawning were observed at Aldabra in the western Indian Ocean.

Cetoscarus bicolor (Rüppell)

Plates 1G,H; 6I

Scarus bicolor Rüppell, 1829: 82, pl. 21, fig. 3 (type locality, Jeddah).

Scarus pulchellus Rüppell, 1835: 25, pl. 8, fig. 3 (type locality, Jeddah).

Scarus ocellatus Valenciennes in Cuvier & Valenciennes, 1840: 278 (type locality, Caroline Islands).

Scarus rosiceps Valenciennes in Cuvier & Valenciennes, 1840: 279 (type locality, Caroline Islands).

Callyodon scriptus Gronow in Gray, 1854: 85 (type locality, Indian Ocean).

Pseudoscarus nigripinnis Playfair & Gunther, 1867: 105, pl. 15, fig. 2 (type locality, Zanzibar).

Scarus ophthalmistius Herre, 1933: 21 (type locality Jolo, Philippine Islands).

Material examined. One specimen, One Tree Island, AMS I.15685-039; one specimen, Ayr, QM I.12731; three specimens, Heron Island, and one specimen, One Tree Island, not retained; two specimens, Lizard Island, to be deposited AMS.

Diagnosis. Median predorsal scales 4–7, subequal, anterior scales often partly embedded; 3 rows of scales on cheek, upper with 7–8 scales, not extending above lower edge of eye, middle row with 6–8, lower row with 3–6; interopercle with 2 longitudinal rows of scales (1 row on other Scarinae); pectoral rays 14–15; lips largely covering dental plates, rows of fused teeth on dental plates clearly visible, no canine teeth on dental plates; each upper pharyngeal bone with three longitudinal rows of molariform teeth, outer row rudimentary, inner rows of teeth not interdigitating; posterior nostrils of adults large.

Colour pattern. Juvenile: body white with broad, dark-edged orange bar on head enclosing eye and most of postorbital head, snout pale brownish; dorsal and anal fins white, large orange-margined black spot on anterior dorsal fin; pectorals and ventrals pale orange to yellow; caudal white with upper and lower margins light orange.

IP: body above level of eye yellow, below abruptly dark brownish, scales edged with black, centres with small black dots and short irregular lines (body colour may vary to light grey so dark scale markings stand out in sharp relief); head light brown with series of small dark dots on lower opercular membrane and throat; fins reddish to purplish brown; caudal with medial posterior region pale yellowish; pectorals brownish, central regions paler; pelvics darker brown; iris orange, dental plates white.

TP: body green, edges of scales orange; scales on anterior half of body with small orange spots; ventral part of head, thorax and abdomen yellow to orange; an area of lower cheek, side of thorax below pectoral fin base, and abdomen darker green; snout, occiput and cheek green with numerous small orange dots; lower lip narrowly green with orange bar on chin, upper lip orange, then green bounded above by an additional orange bar, an orange line from edge of upper lip to pectoral base and continuing ventrally across side of abdomen to level of vent; eye with 1–2 orange postorbital lines; iris orange, dental plates white; dorsal fin green becoming yellowish toward distal margin with orange blotch on each interradiial membrane, distal margin darker green; anal fin yellowish orange with broad blue-green distal margin; caudal fin orange with

crescentic green area, distal margin with thin green line, upper and lower lobes orange with green outer margins; pectoral fins with dark bluish rays and clear membranes, axilla of fin bright yellow; pelvic fins yellow with blue lateral margin. This colour description refers to freshly collected specimens. In life, orange areas of colour pattern are bright pink.

Remarks. This species was placed in the genus *Bolbometopon* by some authors (Rosenblatt & Hobson, 1969; Schultz, 1969). The status of the genus *Cetoscarus* and the synonymy of *C. bicolor* is discussed by Randall & Bruce (1983).

Cetoscarus bicolor is a widely distributed scarid ranging from the Red Sea to the central Pacific. It is distributed along the entire length of the Great Barrier Reef on mid and outer reefs where it generally occurs in pairs on reef crest areas, but larger groups (up to 15) may be encountered on outer barrier reefs. It has not been recorded from Western Australia. *Cetoscarus bicolor* is a large scarid with terminal males reaching 460 mm SL on the southern Great Barrier Reef.

In December 1982 the senior author observed a group of 15–20 IP individuals assembling at an exposed point on Yonge Reef in apparent preparation for spawning. During reproduction, terminal males swim rapidly with the jaws open.

Hipposcarus longiceps (Valenciennes)

Plates 11,J; 6B.

Scarus longiceps Valenciennes in Cuvier & Valenciennes, 1840: 241 (type locality, Waigeu).

Scarus macrocheilos Bleeker, 1854a: 60 (type locality, Halmahera).

Scarus harid (not Forsskal).—Schultz, 1958: 50, pl. 9B.

Hipposcarus schultzi Smith, 1959: 277, fig. 8 (type locality, Philippines).

Material examined. Two specimens, One Tree island, AMS I.15637–044, I.20578–005; one specimen, Lizard Island, AMS I.15637; two specimens (juveniles), Lizard Island, AMS I.25783–001, I.25798–001; one specimen, Half Mile Pass, Great Barrier Reef, BPBM 30886; one specimen, Port Moresby, BPBM 15893; one specimen, Fanning Island, BPBM 7597; seven specimens, One Tree Island, not retained.

Diagnosis. Median predorsal scales 4, scales subequal; 3 rows of cheek scales, upper row 6–8 scales, middle row 5–7 scales, lower row 3–6 scales, these in small triangular patch on cheek; pectoral rays 15; dental plates narrow, their height about 1.5–2.0 in orbit diameter, outer surface smooth, lips covering dental plates, terminal phase with 1–2 canines on upper dental plate; each upper pharyngeal bone with about 8 ridged molariform teeth and an outer row of rudimentary teeth; nostrils exceedingly small; head with sharply pointed profile; caudal fin strongly double emarginate with very short lobes.

Colour pattern. Juvenile: body yellowish grey, scales with darker dots and small lines, these more pronounced

dorsally; abdomen pale yellowish; head and snout brownish; longitudinal pink to red band from tip of snout, through lower portion of eye, extending down side of body to caudal peduncle; posterior region of caudal peduncle yellowish with prominent black spot at termination of longitudinal red band; dorsal and caudal fins brownish, anal fin yellowish brown, pectorals hyaline, pelvics whitish; iris yellow. Outline of longitudinal band present in alcohol preserved specimens.

IP: body pale uniform grey; dorsal scales with faint dark vertical lines; abdominal scales with faint bluish markings; caudal peduncle yellowish; snout and head brownish, upper lip yellowish orange with fine blue border, extending backward as yellow-orange line to point just anterior to orbit; lower lip light bluish; chin and isthmus faintly reddish, cheeks paler; upper margin of orbit light blue; iris yellow; posterior margin of operculum adjacent to pectoral base light orange-yellow; dorsal and anal fins yellow with faint medial blue longitudinal line, distal margin of fins blue; remainder of dorsal fin hyaline; caudal fin yellow, base and upper and lower margins pale blue; upper rays of pectoral light blue, then yellowish orange bar; pelvics pale yellowish, anterior and posterior margins faintly blue. Underwater observations of IP individuals gives the impression of a uniform grey fish with distinct yellow caudal fin and peduncle, with the yellow of the caudal peduncle extending on to dorsum below last 5–6 dorsal rays.

TP: body bluish dorsally, becoming yellowish on sides; scales of dorsum with light orange vertical bars; thorax and lower abdomen bluish; three most ventral scale rows of abdomen with rows of blue blotches, these being restricted to an area posterior to pectoral fin; caudal peduncle yellowish; snout and occiput bluish green, cheek paler; upper lip orange, lower lip bluish, 1–2 small blue postorbital lines; dorsal and anal fins orange-yellow with vertical blue blotch on each fin membrane, these becoming fainter posteriorly, distal margins of these fins blue; caudal membranes orange-yellow with thin blue basal line; upper and lower caudal rays faintly bluish, remaining rays bluish, posterior margin of caudal fin light blue; upper pectoral rays bluish, followed by an orange bar, remainder of fin hyaline; pelvics light bluish, posterior margin darker blue. Viewed underwater, TP individuals have greenish caste with pinkish colouration on head. Blue markings on vertical and pectoral fins appear purple.

Remarks. This species is a member of a distinctive genus of scarids characterised by a pointed head, narrow dental plates and the cheek scales reduced to a small subtriangular patch. The cheek scales themselves are small, often irregularly arranged in rows and some difficulty may be experienced in obtaining accurate counts in small specimens. Members of the genus occur in the Red Sea and Indian Ocean, through to the western and central Pacific. Details of the Red Sea and Indian Ocean species are provided in Smith (1959), Schultz (1969) and Randall & Bruce (1983). Smith (1959)

subdivided members of this genus into a Red Sea (*H.harid harid*) and Indian Ocean (*H.harid vexillus*) subspecies and an Indo-West Pacific species, *H.longiceps*. *Hipposcarus harid* and *H.longiceps* are clearly distinct (Randall & Bruce, 1983). The status of the subspecies of *harid* is more problematical. They are distinct in a number of features of colour pattern (Randall & Bruce, 1983) and different total numbers and disposition of cheek scales. Schultz (1969, table 3) made counts of the cheek scales of 21 individuals from the Red Sea and 18 from the Indian Ocean. Mean total cheek scales in the Red Sea populations was 18.5 ± 0.4 and Indian Ocean populations 26.0 ± 0.6 . The geographical pattern of species distribution described above is consistent with that seen in a number of other scarid species complexes. Further investigation of the *H.harid* complex is needed.

Hipposcarus longiceps is widespread in the northern tropical Pacific and extends southwards to New Guinea and Australia, and eastwards to the central Pacific. It occurs along the entire Great Barrier Reef and is characteristic of the lagoons and outer slopes of reefs both on the outer shelf and in the Coral Sea. The presence of this species in Western Australia remains to be confirmed. It consistently forms large schools as adults. Juveniles tend to be solitary. A moderately large species, terminal males reaching 400 mm SL on the Great Barrier Reef.

Bolbometopon muricatum (Valenciennes)

Plates 1F; 6A.

Scarus muricatus Valenciennes in Cuvier & Valenciennes, 1840: 208, pl. 402 (type locality, Java)

Material examined. One specimen, Lizard island, AMS I.18755-077; two specimens, 775 and 613 mm Yonge Reef, collected by senior author, both retained by D. Bellwood.

Diagnosis. Median predorsal scales 3-5, scales subequal; 3 rows of cheek scales, upper with 4-6 scales, middle with 5-6 scales, and lower with 1-2 scales; cheek and predorsal scales partly embedded with age; 1 row of scales on interopercle; pectoral rays 16-17; dental plates exposed; rows of fused teeth on dental plates easily discernable, each tooth bearing a small tubercle at proximal apex, surface of each tooth slightly convex, giving a nodular texture to the plates, no canine teeth on dental plates; each upper pharyngeal bone with 3 rows of teeth, outer row rudimentary, inner rows not interdigitating; nostrils of young small; posterior nostril oval, increasing in relative size with age, becoming 3 or 4 times longer than anterior nostril; prominent convexity developing on the head, increasing greatly with size until nearly in vertical alignment with mouth in large individuals; caudal fin rounded in juveniles, double emarginate in adults, lobes only slightly produced.

Colour pattern. This species does not display the usual sex-associated patterns of colour change; it maintains a uniform colouration in adult females and males. There

is a distinct juvenile colour pattern.

Juvenile: body uniform greenish with 5 rows of white spots on body, first at level of third dorsal spine, fifth on caudal peduncle, each row with 2-3 spots; vertical fins slightly darker green, pectorals hyaline yellowish, pelvics greenish; iris yellow, dental plates white; white spots still apparent on individuals up to 300 mm SL at which size head profile is becoming convex.

In alcohol, body colouration is brownish green with numerous small dark spots on body; chin with two dark bars.

Adults: uniform dull green on body and fins, head green with anterior part of hump, snout and chin pink; dental plates white; in life body colouration may be lighter green with darker longitudinal bands running along body; in very large individuals sides of head and occipital regions may display temporary light green colouration.

A.M. Ayling provided notes on colour patterns of individuals engaged in courtship activities. Larger individuals within a group (presumably males) dull green on body, with head and posterior ventral region of body pale greenish white. Vertical and caudal fins also greenish white.

Remarks. This is the largest of all the scarids reaching a size of 1000 mm SL. There appears to be a single species although a thorough examination of material from over the full geographic range should be undertaken. This species is poorly represented in museum collections as it is usually difficult to approach and collect. It occurs in small schools; it is most commonly observed on reef fronts but also ranges over reef crests and flats. It feeds on live coral colonies and on algae. No spawning was observed by the authors, although what appeared to be a group spawning assemblage of 40-50 fish was observed on the outer face of Yonge Reef by the senior author during December 1983. *Bolbometopon muricatum* has a wide distribution extending from the Red Sea to the central Pacific. It reaches Okinawa in the northern Pacific and the Great Barrier Reef in the south.

Bolbometopon muricatum is present on mid- and outer-shelf reefs of the Great Barrier Reef but does not extend into the Swain or Capricorn-Bunker reefs at the southern end (Russell, 1983). A.M. Ayling has provided information on the longitudinal distribution on the Great Barrier Reef gathered during his extensive *Plectropomus* surveys. The farthest south this species was observed was in the Swain Reef Group. Five adults were observed on Reef 21-072 (21°08'S) and the species was moderately common on Elusive Reef (21°06'S). None were observed during surveys of Creal, Little Bugatti, Whitetip and Little Stevens Reefs off MacKay (21°36'S). Small numbers were observed during surveys in the Flinders Reefs, Herald and Lihou Cays in the Coral Sea. *Bolbometopon muricatum* has not been recorded from Western Australia.

Scarus altipinnis (Steindachner)

Plates 5I,J; 6F; 10A,B,C

Pseudoscarus altipinnis Steindachner, 1879: 18 (type locality, Kingsmill Islands).*Callyodon waitei* Seale, 1906: 60, fig. 16 (type locality, Tahiti).*Pseudoscarus altipinnis*.—Gunther, 1909: 326, pl.160.*Pseudoscarus brevifilis* Gunther, 1909: 327, pl.161 (type locality, Tahiti).*Scarus chlorodon*.—Schultz, 1969: 26 (In part).

Material examined. HOLOTYPE of *Callyodon waitei* Seale BPBM 1408 320 mm SL; three specimens, Cape Cleveland, QM I.15998, I.16003, I.6894; one specimen, Heron Island, AMS I.15679-049; five specimens (juveniles), Lizard Island, I.25791-001, I.25795-001, I.25403-001, I.25909-001, I.25911-001; one specimen (juvenile), Younge Reef, AMS I.25912-007; ten specimens, Heron Island, not retained.

Diagnosis. Median predorsal scales 5–6; 3 rows of cheek scales, upper row with 6–7 scales, middle row with 6–8 scales, ventral row with 1–3 scales; pectoral rays 15; dental plates exposed, dark green in both colour phases; 1–2 canines on upper dental plates of adults; spinous portion of dorsal fin distinctly higher than soft dorsal, fin membrane covering last few spinous dorsal rays and first soft ray as an extended filament; caudal fin of adults double emarginate, lobes produced as filaments in adults.

Colour pattern. Juvenile: body greyish brown, caudal peduncle abruptly paler, 3–4 vertical series of white dots on sides of body; snout and iris yellow, dental plates pale; dorsal and anal fins with distinctive black and white mottling, pectorals hyaline light yellowish, caudal hyaline whitish, pelvic light grey.

IP: body reddish brown, sides of body posterior to pectoral fin tip with series of small distinctive white dots, these arranged roughly in 3–4 vertical series of 2–3 dots, this pattern becoming more diffuse in adults; dorsal, anal and pelvic fins light reddish brown with bluish distal margins, pectoral light brownish, caudal reddish brown; iris yellow, dental plates dark green.

TP: body dark greenish, distal margins of body scales with darker green bars, these more pronounced on posterior ventral regions of body, abdomen and thorax; isthmus lighter greenish brown, scales on abdomen, base of anal fin and ventral portion of caudal peduncle with scattered greenish spots; occiput and upper snout dark green, a dark green suborbital line, cheeks paler becoming light orange ventrally marked with greenish flecks and dots, operculum with scattering of green dots, snout becoming orange, upper lip orange with a dark green bar, lower lip orange, chin with two dark green bars; dorsal fin greenish brown, the membranes investing each spine and ray dark green, base and distal margin of fin dark green; anal fin greenish brown with extensive and irregular green outer margin, medial region of fin with series of dark green blotches, these becoming more pronounced posteriorly; caudal fin brownish green, dorsal and anal lobes paler, dorsal and ventral margins dark green, posterior margin paler, medial area of caudal fin with dark greenish blotches;

pectoral fins brownish green, upper margin dark green; pelvics pale greenish, spine and anterior ray dark green; iris orange, dental plates dark green. In life, often a broad vertical dusky band in centre of body (Plate 10 C), with colouration anterior to this slightly paler. This dusky band intensified during reproductive behaviour.

Remarks. *Scarus altipinnis* is a member of a complex of three large scarids characterised by a relatively large body depth, strongly lunate caudal fins and an acute snout. The complex includes *S.falcipectus* which is confined to the Indian Ocean from the Seychelles to the west; *S.prasiognathus*, Indian Ocean eastwards from the Maldiv Islands, Indonesia, Philippines to the Ryukyu Islands and Palau; and *S.altipinnis* through the west, central, and southern Pacific. Large *S.altipinnis* may be readily separated from other members of this complex by the characteristic extension of the dorsal fin membrane at the last spine and first soft ray.

Scarus altipinnis has been identified most recently as *S.brevifilis* and prior to this *S.chlorodon*. *Scarus chlorodon* is in fact a synonym of *S.prasiognathus* (see Randall & Choat, 1980). Since 1980 almost all identifications of *S.altipinnis* from Pacific and Australian waters have referred this species to *S.brevifilis*. Schultz (1969) included both *S.altipinnis* and *S.waitei* (Seale) within the synonymy of *S.chlorodon*. However both these species have central and southern Pacific type localities and were considered unlikely to be *S.prasiognathus*. The description of *S.altipinnis* by Steindachner (1879) clearly refers to the Pacific scarid previously identified as *S.brevifilis* (Gunther). The original description suggests that Steindachner may have been uncertain about the distinction between *S.altipinnis* and *S.janthochir* (a synonym of *S.prasiognathus*) but the name has been recognized and used by other workers. Gunther (1909) recognized both *S.altipinnis* and *S.brevifilis*. It is clear from his illustrations that he had identified the terminal (*S.altipinnis*) and initial (*S.brevifilis*) phases of this species although he was unaware of the sexual dichromatism. *Scarus altipinnis* is a valid earlier name for the west and central Pacific scarid previously identified as *S.brevifilis*. The holotype of *Callyodon waitei* Seale was examined by the junior author and was also found to be *S.altipinnis*.

There are a number of informal records of *S.janthochir* (a synonym of *S.prasiognathus*) from Australia. As far as we can determine, these all refer to *S.altipinnis*, although it is possible that *S.prasiognathus* does occur in north-western Australia. Munro (1967) recorded *S.chlorodon* from New Guinea. We are unable to determine from the description whether this refers to *S.altipinnis* or *S.prasiognathus*.

Scarus altipinnis is generally a schooling scarid, common on the outer-shelf reefs of the Great Barrier Reef and the reefs of the Coral Sea, feeding in large groups on reef crests. On mid-shelf reefs smaller groups occur, often associated with very large TP individuals. A small proportion of IP fish were found to be primary

males. Pair spawning involving a very large (approximately 500 mm SL) TP male was briefly observed at Lizard Island. Prior to spawning, the male swam in a highly characteristic fashion with the posterior region of the body arched downward and the filament on the dorsal fin projecting backward. This species shows a wide size range for the terminal colour phase (200–450 mm SL at Heron Island). It is one of the larger scarids on the Great Barrier Reef.

Scarus bleekeri (de Beaufort)

Plates 4A,B; 8I,J

Scarus Quoyi (not Valenciennes).—Bleeker, 1853b: 607 (Ternate).

Pseudoscarus Quoyi (not Valenciennes).—Bleeker, 1862: 29, pl. 6, fig. 3.

Callyodon bleekeri de Beaufort, 1940: 318 (new name for *Scarus quoyi* Bleeker, 1853, not Valenciennes).

Scarus troscheli.—Schultz, 1969: 21 (in part).

Material examined. Four specimens, Madang, AMS I.17090–023, I.18090–023, I.17088–044; one specimen, Fiji, BPBM 11404; one specimen, Heron Island, USNM; one specimen (juvenile), Yonge Reef, AMS I.25792–001; two specimens Lizard Island (juveniles), AMS I.25903–002, I.25916–001.

Diagnosis. Median predorsal scales 4; scale rows on cheek 2, both with 6–8 scales; pectoral rays 15; caudal fin truncate in both colour phases; dental plates not covered by lips; 1–2 canines posteriorly on side of upper dental plates of adults.

Colour pattern. IP: body dark brown, edges of scales narrowly orangish, shading to dull orange-red on abdomen and thorax; body with faint greenish yellow bars, these numbering 3–4 with anterior one predorsal, bars extending only to body mid-line; posterior caudal peduncle and base of caudal fin greenish yellow, in small IP individuals caudal peduncle pale yellow to white, fading to orangish brown on death (also fading, a yellowish wash on upper half of head); upper lip with narrow margin of salmon pink and submarginal band of dull blue-green; lower lip and chin salmon pink with three transverse dull blue-green bands that join to median dull blue-green band ventrally; fins orangish to reddish brown, dorsal and anal with faint median longitudinal dark band and narrow dark margin; pectoral membranes pale; pelvics with dark lateral margin; dental plates white; eye orange-yellow. Viewed underwater, IP individuals characteristically show irregular lighter bars against dark body colouration, the bars fading rapidly on death. Preserved specimens uniform brownish with lighter caudal peduncle; bands on chin usually still visible. Care must be taken to differentiate these from IP *S.sordidus* in preserved collections.

TP: scales of body green with vertically elongate rosy salmon bar, except abdomen and thorax green, and anterodorsally body and nape yellowish; large whitish area on cheek bordered by blue-green; lips faintly

salmon, band of this colour continuing from rictus to lower edge of eye and along upper edge of large pale area on cheek; transverse turquoise band on upper lip and 2 on chin; green band extending anteroventrally and 2 posterodorsally from eye; dorsal fin salmon with blue margin, green at base, with median longitudinal green band; anal fin blue-green basally, turquoise distally, the 2 regions separated by band of salmon; caudal fin turquoise with salmon band in each lobe and short streaks of this colour centrobasally; pectoral fins largely turquoise with streak of salmon in upper part and whitish at base; pelvic fins pale salmon with blue lateral margin; dental plates greenish. In preserved specimens, characteristic cheek marking highly visible and there are no difficulties associated with identification in museum collections.

Remarks. This species is similar to *Scarus troscheli* Bleeker and was regarded by Schultz (1969) as a junior synonym of that species. The taxonomic history of *S.bleekeri* and *S.troscheli* plus details of their distribution patterns are discussed in Randall & Choat (1980). *Scarus bleekeri* is relatively rare on the Great Barrier Reef. It was not included in any of the major surveys of shelf and Coral Sea reefs carried out by A.M. Ayling and D. Williams but was observed occasionally on the slopes of mid- and outer-shelf reefs. It was observed most frequently in more sheltered reef habitats with abundant coral growth, typically in deeper water. The authors have observed both colour phases as solitary individuals and small groups over much of the Great Barrier Reef. Very small IP individuals may be confused with small *S.sordidus*. This species has not been recorded from northern or western Australia.

Scarus chameleon n.sp.

Plates 3C,D; 9D,E,F,G,H

Scarus lunula (not *Callyodon lunula* Snyder).—Choat & Robertson, 1975: 264–267 (Heron Island, Great Barrier Reef)

Material examined. HOLOTYPE: BPBM 22177, 204 mm SL, TP male, Philippines, Sumilon Island (off southeast Cebu), east side, 20 m, spear J.E. Randall, 26 August 1977.

PARATYPES: AMS I.15470–001, 211 mm SL, TP (eviscerated), Australia, Queensland, Great Barrier Reef, Capricorn Group, Heron Island, 23°27'S, 151°57'E, spear, J.H. Choat, 2 February 1967; BPBM 7425, 136 mm SL, IP female, Belau, outside barrier reef east of Eil Malk, 6 m, spear, J.E. Randall, 10 June 1968; BPBM 9466, 149.5 mm SL, TP male, Belau, Augulpelu Reef, west side, 3.5 m, spear, J.E. Randall, 10 April 1970; BPBM 11649, 159.5 mm SL, TP male, Fiji, Viti Levu, Nukulau Pass off south-east side of Makuluvā Island, 15 m, spear, J.E. Randall, 2 September 1971; BPBM 14517, 2: 151–187 mm SL, IP female and TP male, Great Barrier Reef, Capricorn Group, Heron Island, outer reef flat and reef front, 1–4 m, spear, J.E. Randall, J.H. Choat & D.R. Robertson, 21 January 1973; BM(NH) 1984.4.17.41, 169.5 mm SL, IP female; CAS 54884, 166 mm SL, IP female; USNM 266381, 2: 136–186 mm SL, IP female and TP male—all with same data as BPBM 14517; BPBM 14621, 176 mm

SL, TP male, Fiji, Yanutha Island in Mbengga Lagoon, 4 m, spear, J.E. Randall, 11 March 1973; NTM S11158-001, 189 mm SL, TP male, Great Barrier Reef, Carter Reef, outside reef, 6 m, spear, J.E. Randall, 25 June 1973; AMS 1.20572-014, 193 mm SL, TP male, Great Barrier Reef, Capricorn Group, One Tree Island, 6 m, explosives, B.C. Russell and party, 23 November 1973; NSMT-P 23034, 205 mm SL, TP male, Ryukyu Islands, Okinawa, Sesoko Island, west side, 10 m, spear, J.E. Randall, 1 June 1975; AMS I.21997-001, 137.5 mm SL, IP female, Great Barrier Reef, Yonge Reef, 27 m, explosives, B.C. Russell and party, 1 November 1975; BPBM 29403, 161 mm SL, IP female, same data as holotype; MNHN 1984-418, 149.5 mm SL, TP male, Philippines, Cebu City market, J.E. Randall, G.W. Tribble, R. Rutherford & K.E. Carpenter, 31 July 1978; QM I.14902, 248 mm SL, TP male, Queensland, Flinder's Reef (off Cape Moreton), spear, M. McDade, 24 September 1978; QM 16006, 210 mm SL, TP male, Great Barrier Reef, Capricorn Group, North West Island, spear, M. McDade, May 1979; BPBM 27840, 90.4 mm SL, Great Barrier Reef, Lizard Island, off Granite Bluff, 13 m, spear, J.E. Randall, 20 September 1981; BPBM 29401, 2: 165.5–175.5 mm SL, IP females, Great Barrier Reef, Lizard Island, point at north end of Coconut Beach, outer edge of fringing reef, 4–12 m, spear, J.E. Randall, 8 December 1982; WAM P.28275-001, 168 mm SL, IP female, same data as preceding; BPBM 29402, 134 mm SL, IP female, Great Barrier Reef, MacGillivray Reef (near Lizard Island), 4 m, spear, J.H. Choat, 11 December 1982 (see Table 8).

Additional material examined. One specimen, Sydney Harbour, AMS I.17740-003; one specimen, Heron Island, QM I.6841; five specimens, Lizard Island, AMS I.18767-032, I.19445-014,

I.19455-016, I.19461-004; eight specimens (juveniles), Lizard Island, AMS 1.25799-001, 1.25793-001, 1.25782-002, 1.25904-001; one specimen, Yonge Reef, QM I.14867; one specimen, Kenn Reef, AMS IB.4892; one specimen, Kendrew Island, Western Australia, WAM P.24636-001; one specimen, Abrolhos Island, WAM unregistered; one specimen, Madang, AMS I.17088-066; 21 specimens, Lizard Island, not retained.

Diagnosis. Median predorsal scales 4, preceded by pair of moderately large, laterally overlapping scales; rows of scales on cheek 3, upper two of 6–7 (rarely 8) scales, and lower of 1–3 scales; pectoral rays 14; gill rakers 39–46; lips covering $\frac{3}{4}$ to all of upper dental plate and $\frac{1}{2}$ – $\frac{3}{4}$ of lower dental plate; terminal males with 1–2 canine teeth posteriorly on dental plates, and IP fish with 0–1 canines on dental plates; nostrils small; dorsal profile of head of large terminal males with slight convexity in interorbital space; body depth 2.5–2.8 in SL; head length 2.75–2.9 in SL; snout 2.5–2.95 in head; orbit diameter 5.3–7.35 in head; caudal fin of IP slightly rounded to slightly emarginate, of TP males emarginate to lunate, the maximum caudal concavity 3.5 in head; pectoral fins 1.35–1.55 in head; pelvic fins 1.85–2.2 in head.

Colour of IP when fresh: brown, lower third of body often abruptly lighter brown; dorsal fin orangish brown with violet-grey margin; unscaled part of caudal fin brownish yellow.

Colour of TP when fresh: broad zone of salmon pink on lower side of body extending posteriorly from behind

Table 8. Proportional measurements of type specimens of *Scarus chameleon* expressed as a percentage of the Standard Length

	Holotype		Paratypes								
	BPBM 22177 TP ♂	BPBM 27840 juv	AMS I.21997-001 IP ♀	BPBM 9466 TP ♂	BPBM 29403 IP ♂	BPBM 29401 IP ♀	BPBM 29401 IP ♀	BPBM 14517 IP ♀	AMS I.20572-014 TP ♂	NSMT-P 23034 TP ♂	AMS I.15470-001 TP ♂
Standard length (mm)	204	90.4	137.5	149.5	161	165.5	175.5	187	193	205	211
Body depth	39.9	36.4	35.5	39.4	39.4	36.4	37.2	36.8	37.0	38.3	36.0
Body width	17.2	17.6	17.3	18.3	16.8	18.0	18.5	17.0	16.5	17.6	16.6
Head length	36.7	35.9	35.7	36.3	36.0	34.5	36.5	36.1	34.7	36.1	36.2
Snout length	14.5	12.6	12.2	13.7	13.5	13.7	13.6	14.2	13.3	13.7	14.1
Orbit diameter	5.1	6.8	5.8	5.7	5.5	5.4	5.7	5.2	4.9	4.9	5.0
Interorbital width	12.1	11.9	10.8	11.1	11.2	12.2	11.1	11.7	11.4	12.1	11.1
Caudal peduncle depth	15.6	aberrant	15.1	16.1	15.5	15.1	15.6	14.9	14.9	15.6	14.8
Caudal peduncle length	13.3	13.5	13.2	12.7	12.5	13.0	13.4	13.1	12.4	12.2	12.0
Predorsal length	35.8	35.0	34.8	36.1	34.1	34.9	34.8	34.8	34.0	34.5	35.2
Preal length	66.9	64.5	67.2	68.1	65.8	63.8	63.5	67.0	67.5	68.7	68.8
Prepelvic length	36.8	36.5	36.8	37.4	36.7	35.5	37.0	37.8	36.4	37.0	37.5
Dorsal fin base	58.2	57.2	56.1	57.7	59.4	58.8	59.3	58.8	57.0	58.8	58.1
Length 1st dorsal spine	9.8	12.2	12.2	11.2	10.8	9.3	10.2	11.4	11.4	11.6	11.7
Length 9th dorsal spine	11.2	13.3	13.6	12.7	11.6	10.8	11.1	11.6	12.3	12.6	12.5
Length longest dorsal ray	12.3	14.3	14.1	13.4	12.4	13.0	12.0	13.7	12.4	12.7	12.7
Anal fin base	26.1	26.6	23.0	24.6	26.0	26.9	27.0	26.5	25.7	25.4	25.1
Length 3rd anal spine	9.8	11.9	11.5	10.7	10.1	9.8	9.4	10.6	10.1	10.5	9.5
Length longest anal ray	11.8	13.9	13.0	11.5	11.8	12.1	11.8	11.6	10.2	12.1	12.3
Caudal fin length	27.2	22.7	23.4	24.0	23.0	20.4	21.6	25.0	27.0	24.5	26.0
Caudal concavity	10.3	0	3.7	4.2	2.6	0	2.6	6.3	4.9	5.7	5.1
Pectoral fin length	24.6	24.8	25.3	25.0	23.6	25.2	23.4	23.5	23.8	24.0	24.4
Pelvic spine length	12.5	14.7	14.7	13.7	12.4	13.3	13.7	14.3	12.2	13.9	11.3
Pelvic fin length	16.5	18.0	19.2	18.1	16.7	16.0	17.2	18.1	17.2	18.5	17.6

head; scales of body above and posterior to this zone about half blue-green and half salmon pink, below largely pale blue-green; head with green band crossing upper interorbital space; caudal fin orange with blue upper and lower margins, and large D-shaped mark of green and blue-green centroposteriorly in fin; pectoral fin pale orange with blue band at base connected to blue upper margin of fin.

Description (based on holotype and ten paratypes). Dorsal rays IX, 10; anal rays III, 9; pectoral rays 14 (uppermost ray rudimentary, second ray unbranched); pelvic rays I, 5; principal caudal rays 13, uppermost and lowermost unbranched; upper procurrent caudal rays 7; lower procurrent caudal rays 7; lateral line interrupted, dorsoanterior portion with 18 (17–19) tubed scales (tubules mostly branched) and peduncular part with 6 (4–6) (plus 2 tubed scales on caudal fin base, last greatly enlarged); scales above lateral line to origin of dorsal fin $1\frac{1}{2}$; scales below lateral line to origin of anal fin $5\frac{1}{2}$; median predorsal scales 4, these preceded by pair of laterally overlapping scales about $\frac{3}{4}$ width of predorsal scales; median predorsal scales slightly larger posterior to anterior, the most posterior deeply indented for first dorsal spine; scale rows on cheek 3, upper row with 7 (6–8, rarely 8) scales, middle row with 7 (6–8, rarely 8) scales, and lower row with 2 (1–3, usually 2, rarely 1) scales; circumpeduncular scales 12; gill rakers 41 (39–46 in 10 paratypes); branchiostegal rays 15; vertebrae 11 + 14 (holotype and one paratype).

Body moderately deep, depth 2.5 (2.55–2.8) in SL, and compressed, width 2.3 (2.0–2.35) in depth; head length 2.75–2.9 in SL; head moderately pointed, dorsal and ventral profiles of IP and small TP fish about equally convex, but large terminal males, such as the holotype, have slight protuberance in dorsal profile over interorbital space; snout 2.55 (2.5–2.95) in SL; orbit diameter 7.2 (5.3–7.35) in head; interorbital space very convex, least width 3.05 (2.85–3.3) in head; caudal peduncle deeper than long, least depth 2.35 (2.25–2.45) in head.

Mouth slightly inferior, gape slightly oblique; teeth fully fused to form relatively thin, beak-like, dental plates, surfaces of which are smooth; median suture in each dental plate; margin of plates slightly irregular; 2 canine teeth projecting laterally (slightly ventroposteriorly) posteriorly from side of upper dental plate near free margin (1–2 on TP paratypes; 0–1 on IP paratypes); 1 lateral canine posteriorly on lower dental plate (1–2 on TP paratypes; 0–1 on IP paratypes); upper lip covering $\frac{3}{4}$ to all of upper dental plate, and lower lip covering $\frac{1}{2}$ – $\frac{3}{4}$ of lower dental plate.

Upper pharyngeal bones each with row of 10 ridged molariform teeth (cusps of posterior teeth flattened by wear) which interlock medially and lateral row of small rudimentary molariform teeth which alternate with ridged molars; lower pharyngeal bone with concave elliptical surface of interdigitating molariform teeth in 5 transverse rows of 15, first three transverse rows distinctly ridged, the rest worn nearly flat (pharyngeal mill dissected from 176 mm paratype).

Nostrils very small, anterior in short membranous tube, in front of upper edge of pupil about $\frac{1}{3}$ horizontal distance to front of snout; nostrils close together, internarial space about $\frac{2}{3}$ pupil diameter.

Scales large, cycloid, extending dorsally on head to mid-interorbital space; fins naked except for upper row of scales on body which extend broadly onto base of dorsal fin (except posteriorly) and 2 vertical rows of scales basally on caudal fin; scaly process of 2 scales (more posterior one pointed) mid-ventrally at base of pelvic fins; slender pointed axillary scale at lateral edge of pelvic fin base about $\frac{3}{4}$ length of pelvic spine.

Origin of dorsal fin directly above upper end of gill opening; dorsal fin continuous with no notch between spinous and soft portions; dorsal and anal spines slender and flexible, tips curving posteriorly; first dorsal spine 3.7 (2.95–3.7) in head; second to ninth dorsal spines subequal, ninth 3.3 (2.65–3.3) in head; seventh to ninth dorsal soft rays longest, 3.0 (2.5–3.05) in head; first anal spine very slender, about $\frac{1}{2}$ length of second spine; second anal spine about $\frac{3}{4}$ length of third spine; third anal spine 3.75 (3.0–3.9) in head; third to seventh anal soft rays longest, 3.1 (2.6–3.4) in head; caudal fin slightly rounded to slightly emarginate in IP fish, emarginate to lunate in TP males, its length 1.35 (1.3–1.7) in head; caudal concavity of holotype 3.55 in head; third or fourth pectoral ray longest, 1.5 (1.35–1.55) in head; pelvic fins 2.2 (1.85–2.2) in head.

Colour of holotype in alcohol: brown, becoming light brown on side of body in a broad zone from behind head to beyond a vertical at origin of anal fin; each lip edged in a narrow pale band, the upper one extending to lower edge of orbit; a transverse narrow pale band at base of upper lip joined to marginal band by a narrow median pale band; median fins light brown, the dorsal with a submarginal translucent band which is wavy on its lower margin (progressively more undulating posteriorly); anal fin with a similar translucent band, but broader and nearer middle of fin; paired fins light brown, the pectorals with a slightly darker upper margin; a crescentic area posteriorly in caudal fin slightly lighter than rest of fin.

Colour of adult IP fish in alcohol: dark brown, slightly paler ventrally; a narrow dark margin on dorsal fin; centroposterior part of caudal fin a little paler than rest of fin; paired fins light brown. A 90.4 mm paratype is brown with the lower half of the head and about the lower third of the body abruptly pale.

Colour of holotype when fresh: scales of back and posterior body orangish with broad vertically elongate blue-green band on each; broad zone of salmon anteriorly on lower side of body between level of eye and lower pectoral base, narrowing and becoming diffuse posteriorly above middle of anal fin; ventral part of head and body largely pale blue-green; lips narrowly edged in bright blue, the band of the upper lip extending to lower edge of eye and continuing as an irregular green band to end of opercle; head above this band light green with lavender cast; transverse dark green band across posterior interorbital space; irregular dark green

markings on nape; irregular horizontal green band extending posteriorly from eye; short transverse narrow blue line on snout at base of upper lip joined by median narrow blue band to blue band on upper lip, the two bands separated by a zone of salmon pink; chin salmon pink with narrow transverse blue band which is joined at right angles to midventral blue band; lower half of head light blue-green suffused with orange; posterior margin of opercle with lower part of opercular flap to level of ventral edge of pectoral fin base with blue-green band; iris brownish orange, becoming blue-green outwardly; dorsal fin green basally with broad blue margin and broad submarginal orange band, the lower edge of which becomes progressively more wavy posteriorly, such that the last few membranes have a tongue of orange extending downward into the green zone nearly to the base; anal fin divided almost equally into basal band of blue-green, middle band of orange (lower edge somewhat wavy) and outer band of blue; basal scaled part of caudal fin coloured like caudal peduncle; unscaled part orange, suffused basally with green, upper and lower borders blue; large D-shaped mark centroposteriorly caudal fin, curved anterior part of 'D' green and vertical posterior part blue (center of 'D' and narrow margin posterior to it orange); pectoral fins with salmon pink rays, pale membranes, and blue-green band across base linked to blue-green upper margin; pelvic fins pale yellowish with blue lateral margin.

Colour of a 170 mm IP female when fresh: dark brown, lighter brown ventrally with reddish caste; lower lip and front of chin pinkish; iris brownish orange-red; unscaled part of dorsal fin light brownish orange with violet-grey margin; anal fin light reddish brown; unscaled part of caudal fin brownish yellow, lobes darker than centre of fin; pectoral fins with orangish brown rays, pale membranes; dark bluish grey band across base joining band of same colour along upper edge of fin about $\frac{2}{3}$ distance to tip; pelvic fins light pinkish with 3 indistinct small purplish spots along lateral edge.

Colour of a 90.4 mm paratype when fresh: upper $\frac{2}{3}$ of body brown, lower $\frac{1}{3}$ abruptly light reddish grey; caudal fin brownish yellow; dorsal fin orangish brown; anal fin reddish brown; two reddish brown transverse bands on chin.

Colour of a 23 mm juvenile when fresh: head brown; body grey, shading to brown posteriorly, with 5 longitudinal rows of white spots, those in upper row (level of upper end of gill opening) and third row (level of upper edge of pectoral base) as 4 or 5 close-set pairs; 2 transverse brown bands on chin; base of pectoral fins yellow; iris brownish yellow.

Remarks. This species is named *chameleon* in reference to its ability to rapidly change colour. The basic colour pattern of IP individuals is that of a light greyish to brownish fish becoming paler ventrally with a characteristic yellow caudal fin. This colour pattern may change rapidly, with the mid-body region becoming abruptly darker, providing a striking contrast between

the darker dorsal and paler ventral regions (Plate 9E). A series of yellowish saddles may be superimposed on the the darker mid-body regions. The dorsum adjacent to the fin is slightly paler than the mid-body, and the caudal fin is pale rather than distinctly yellow. A further variant pattern displays a distinct yellow band in the mid-body region extending on to the caudal peduncle and fin (Plate 9F). In all variants of this phase the major impression is of a bicoloured fish with a pale ventral region and an abruptly darker dorsum.

In TP individuals the mid-body region may vary abruptly from bright salmon pink (Plate 9G) to a striking whitish yellow (Plate 9H). With the former pattern the background body colouration is pinkish orange against which the green markings of the head and the blue-green areas on each scale stand out in sharp contrast to the background. Switching of the mid-body colouration to whitish yellow is accompanied by a fading of the pinkish background colouration and a deepening of the green pigmentation of the body providing a striking contrast between the darker dorsal and the paler mid-body regions. These changes may occur abruptly in the same individual over a very short time period and without any overt interactions with other individuals.

Scarus chameleon occurs in a wide variety of habitats from the outer part of reef flats at depths of 1 m or less to at least 30 m on reef slopes, and from protected localities such as bays and lagoons to exposed outer reef areas. This scarid is of moderate size; the largest we have examined is a TP male 248 mm SL from Flinder's Reef, Queensland (QM I.14902). It is a relatively common scarid on the Great Barrier Reef. A series of cross-shelf reef surveys revealed that it is present on both mid- and outer-shelf reefs but more abundant on the latter. It is also present on one reef of the Flinders Reef group, Coral Sea (D. Williams, pers. comm). A Coral Sea survey by A.M. Ayling revealed that this species was moderately common on Herald Cay and Lihou Reef. It is usually observed singly or in small mixed species feeding schools. Over the past three years this species has shown strong recruitment on northern reefs in the Lizard Island area.

Scarus chameleon has a wide distribution within Australian waters. Specimens have been recorded from Western Australia (Abrolhos Is.), Lord Howe Island, Flinders Reef (southern Queensland) and a confirmed record of a single juvenile from Sydney Harbour. Choat & Robertson (1975: Table 1A) examined the gonads of 25 specimens of *S. chameleon* (identified as *S. lunula*) from Heron Island, Great Barrier Reef. Thirteen were IP females, one was an IP male (primary male), one was a transitional specimen, and 10 were TP males (all secondary males). In this series the smallest sexually mature female measured 115 mm SL. Our adult type specimens included 11 IP fish, all females, the largest 175.5 mm SL, and 13 TP males, the smallest 149.5 mm SL.

This species is close to *S. festivus* Valenciennes (*S. lunula* is a synonym—see Randall & Bruce, 1983).

The two have the same meristic data; *S. festivus* even has the overlapping pair of scales in the median line anterior to the predorsal series of four scales. The colour patterns of the two are also similar. The easiest way to distinguish them is the more pronounced convexity of the forehead of *S. festivus* at any one size. This hump appears early on *S. festivus* and becomes marked in terminal males, whereas it is only slightly developed on large TP males of *S. chameleon*. *Scarus festivus* does not have the distinctive brown bicoloured pattern of the IP of *S. chameleon* in life. The TP of *S. festivus* differs in lacking the broad salmon zone on the side of the body and in having two green bands crossing the interorbital space (one broad one posteriorly as in *S. chameleon*, plus a narrower one nearly parallel to it in the anterior interorbital). Also, the caudal fin of *S. festivus* has a solid crescentic blue-green band posteriorly in the caudal fin, in contrast to the D-shaped marking of *S. chameleon*.

Scarus festivus and *S. chameleon* overlap over much of the range of the latter, but *S. festivus* extends its range westward to East Africa and east to French Polynesia while *S. chameleon* appears to extend further into southern Pacific waters. Masuda et al. (1984) identify and record *S. festivus* but not *S. chameleon* from the Ryukyu Islands. However Masuda (1984) provides a colour photograph of a TP *S. chameleon* (identified as TP *S. ghobban*) from Kerama Island, south-west Okinawa. Any specimens collected in northern or western Australia should be carefully checked to determine whether they are in fact *S. festivus*.

Scarus dimidiatus Bleeker

Plate 41, J

Scarus dimidiatus Bleeker, 1859: 17 (type locality, Doreh, New Guinea).

Callyodon zonularis Jordan & Seale, 1906: 321, fig. 60 (type locality, Pago Pago, American Samoa).

Pseudoscarus caudifasciatus var. *zonularis* Gunther, 1909: 312, pl. 153, fig. B (Ponape).

Callyodon fumifrons Jordan & Seale, 1906: 326, pl. 34 (type locality, Pago Pago, American Samoa).

Material examined. One specimen, Heron Island, AMS I.15481-001; one specimen, Swain Reefs, QM I.11410; one specimen, Escape Reef, AMS I.22631-033; one specimen, Solomon Island, AMS I.15630-153; one specimen (juvenile), Lizard Island, AMS I.25785-002; one specimen (juvenile), Yonge Reef, AMS I.25912-006.

Diagnosis. Median predorsal scales 6 (rarely 5); rows of scales on cheek 3, upper row with 6-7 scales, middle row with 6-8 scales, lower row with 1-4 scales; pectoral rays 14; caudal fin slightly rounded to truncate; dental plates usually covered or nearly covered by lips; no canine teeth on sides of dental plates.

Colour pattern. IP: body yellowish, shading to whitish ventrally, with 5 slightly diagonal dark grey-brown bars on upper half of body which are broader than yellow interspaces: first at origin of dorsal fin extending onto nape where dark colour merges with

brown-grey of rest of upper half of head; the last, rather indistinct, dorsally on caudal peduncle; 3 whitish longitudinal lines on abdomen following centres of scale rows; broad near-horizontal band of dark brown extending posteriorly from eye to end of opercular membrane; head below this band, and a continuing demarcation from lower edge of eye to corner of mouth whitish with yellowish cast; dorsal fin pale yellowish grey, upper part of dark bars of body extending onto fin (bars more pronounced on scaled basal portion of fin than on unscaled); anal and pelvic fins whitish; caudal fin yellowish; pectoral fins with yellowish rays (more yellow dorsally than ventrally) and pale membranes. Juveniles coloured much like the initial phase but the ground colour generally a brighter yellow.

TP: upper part of head posterior to mid-interorbital space and anterodorsal part of body to base of seventh dorsal spine solid blue-green; rest of body (except thorax and abdomen which are primarily greenish) blue-green, edges of scales orangish; dark purplish brown band passing from eye to end of opercular membrane just above level of pectoral base; below and adjacent to this a salmon pink band, edged in blue-green, this band continuing in solid blue-green to corner of mouth where it expands to a broad area on front of snout and on chin; edge of upper lip narrowly salmon; dorsal part of snout above blue-green anterior area to mid-interorbital space lavender-grey; dorsal fin coloured like body on basal scaled portion, margin broadly blue, with broad middle zone of salmon bisected by green longitudinal band which may be broken into series of spots posteriorly; anal fin blue-green with longitudinal band of salmon to lavender just above green scaled basal portion; scaled basal portion of caudal fin coloured like body, unscaled part blue-green with four longitudinal streaks of salmon in central part of fin; pectoral fins blue-green with broad zone to dark purplish in central upper portion; pelvic fins light blue-green on lateral half and greyish lavender on medial half. Pair spawning has been observed at both Lizard and One Tree Islands. During spawning TP individuals show a number of modifications to the colour pattern. Upper anterior dorsum back to level of 7th dorsal spine usually dark blue-green, becoming lilac with yellow blotch below 8th spine; remainder of body blackish grey with pale greenish area on lower caudal peduncle; dark blotch on snout above eye, cheek paler, diagonal markings behind eye prominent; upper and lower lobes of caudal fin light grey. The initial phase show no differentiation during spawning. When spawning, TP colouration shows a number of similarities to spawning TP *S. schlegeli*.

Remarks. The IP of *S. dimidiatus* is very similar in colour to that of *Scarus scaber* Valenciennes. However the TP is distinct. Previous identifications of *S. scaber* from Great Barrier Reef waters all refer to IP *S. dimidiatus*. This species is similar to *S. oviceps* in terms of habitat associations, local distribution and abundance patterns. It is characteristic of sheltered areas but may make local migrations to the reef edge for spawning. In all areas of the Great Barrier Reef this species is

relatively rare, occurring singly or in small groups. It is not usually represented in museum collections or recognised in field surveys. *Scarus dimidiatus* has not yet been recorded from Western Australia, nor does it occur in the list of New Guinea species (Munro, 1967). A.M. Ayling, (pers. comm) observed the IP on Coral Sea reefs and noted that the colour pattern was paler than that seen in shelf reef individuals. Marshall (1965) listed a scarid from the Great Barrier Reef identified as *Callyodon mutabilis*. Schultz (1969) concluded that this record represented *S. scaber*, a western Indian Ocean species. Marshall's description is not detailed enough to allow identification of the scarid referred to as *S. mutabilis* although he may have been referring to *S. dimidiatus*. It is a moderately sized scarid with terminal males reaching 300 mm SL. Pair spawning has been observed at One Tree and Lizard Islands.

Scarus flavipectoralis Schultz

Plates 21,J; 91,J

Scarus flavipectoralis Schultz, 1958: 5, 31, 34, 52, pl. 9D (type locality, Luzon, Philippine Islands).

Material examined. Two specimens, One Tree Island, AMS I.15682-039, I.15684-034; one specimen Rib reef, QM I.7782; eight specimens Lizard Island, AMS I.19108-006, I.19442-005, I.19464-007, I.19469-006, I.19469-009; one specimen, Malatia, Solomon Islands, AMS I.15360-154; one specimen, Espiritu Santo, Solomon Islands, AMS I.17467-024; three specimens (juveniles), Lizard Island, AMS I.25787-001, I.25784-004; three specimens Heron Island not retained.

Diagnosis. Median predorsal scales 4, scales subequal, second scale largest; scale rows on cheek 3, upper row with 6-7 scales, middle row with 5-7 scales, lower row with 1-2 scales (2 specimens with no scales in third row on one side); pectoral rays 14; caudal fin truncate in initial phase (slightly rounded when fin is spread) to slightly lunate in terminal phase; lips nearly covering dental plates; terminal males with 1-2 upward-projecting canines posteriorly on lower dental plate, and 1 posteriorly on upper plate.

Colour pattern. IP: body grey to brown becoming lighter ventrally, head slightly darker, iris yellow, dental plates white; 2 indistinct whitish longitudinal streaks following scale rows on abdomen; dorsal fin yellowish with medial row of bluish spots and bluish distal margin; anal fin brownish grey becoming paler distally; caudal fin dark purplish grey; pelvic fins light bluish with grey leading edge; pectoral fins yellowish hyaline with distinct yellow base except for small dark spot at upper edge. Viewed underwater the initial phase is a uniform pale grey fish characterised by brownish to purple caudal fin and yellow pectoral fin.

TP: body bicoloured, anterior half orange-brown, thorax bluish brown, posterior half green with pink vertical bar on posterior body scales; mid-region of caudal peduncle yellowish, this becoming distinct yellow patch in reproductively active individuals; head brown to orange with broad horizontal green band from front

of snout through lower part of eye to end of opercle, narrow transverse green band on lower lip, broader green band on chin with series of green markings on throat, iris yellow; mid-ventral green band from isthmus to anus; dorsal fin light orange with median row of green spots, some joined anteriorly to form band, scaled basal portion green, margin blue; anal fin light orange with broad blue distal margin; caudal fin light orange with broad blue upper and lower margins and blue centrobasal area in unscaled part of fin; pectoral fins yellowish with distinct green band at base and blackish spot at upper proximal corner; pelvic fins pale orange with blue leading edge; dental plates white.

Remarks. *Scarus flavipectoralis* is characteristic of sheltered or deeper waters on the Great Barrier Reef. It is a relatively small scarid with terminal males rarely reaching 300 mm SL. The reproductive biology of this species is not well known. Pair spawning has been observed; the species is probably weakly diandric, with a small proportion of primary males. It is often seen in small groups at the reef-sand interface and frequently grazes algal material from the sand surface, often in association with *S. schlegeli*. Russ (1984b) described *S. flavipectoralis* as characteristic of back-reef areas on the mid-shelf reefs. It was also observed by A.M. Ayling in back-reef habitats in fish surveys of 12 northern outer-shelf reefs. This species was not observed on Coral Sea reefs during the extensive surveys of A.M. Ayling and D. Williams (pers. comm.). It has not been recorded from northern or western Australia. *Scarus flavipectoralis* appears to be restricted to the western and central Pacific extending to the northernmost Philippines and to the Great Barrier Reef in the south. Masuda et al. (1984) did not record this species from southern Japan.

Scarus forsteni (Bleeker)

Plates 5E,F; 6H; 10E,F

Pseudoscarus forsteni Bleeker, 1861: 238 (type locality, Celebes and Moluccas)

? *Callyodon laxtoni* Whitley, 1948: 94 (type locality, Ocean Island)

Scarus lepidus.—(not Jenyns, 1842) Schultz, 1958: 81, pl.15 C (in part); 1969: 27 pl.5 D (in part).

Scarus tricolor.—(not Bleeker, 1849) Randall & Choat, 1980: 396, figs.11-12 (in part).

Material examined. HOLOTYPE of *Callyodon laxtoni*, Ocean Island, AMS IB.1888; one specimen, One Tree Island, BPBM 14476; two specimens, Lizard Island, AMS IB.19455-017; two specimens, Malatia, Solomon Islands, AMS I.15360-155; one specimen (juvenile), Yonge Reef, AMS I.25908-001; one specimen, Myrmidon Reef, not retained. In addition 14 specimens of *S. forsteni* (BPBM 4770, 6130, 7141, 7143, 8925, 9215, 10896, 12949, 13033, 16597, 16704, 16839, 17123, 17152), and six specimens of *S. tricolor* (BPBM 7739, 7745, 7751, 21610) from western and central Pacific and Indian Ocean localities were examined.

Diagnosis. Median predorsal scales 6 or 7; 3 rows of

scales on cheek, 5–7 scales in dorsal row, 6–9 scales in middle row, and 2–5 in lower row; pectoral rays 14 rarely 13; TP and large IP individuals with 1–2 canines on upper dental plate; dental plates partially covered by lips; caudal fin of initial phase emarginate, of terminal phase strongly emarginate.

Colour pattern. Juvenile: body brownish with 3 dark longitudinal stripes, first from dorsum of head and body to posterior base of dorsal fin, second from tip of snout through eye to base of caudal fin, third from base of pectoral fin to base of caudal fin (this stripe may extend on to operculum); in life a white spot on side at pectoral fin tip; dark bar at pectoral base; upper and lower lips darker brown, brownish bar on chin extending to orbit; dorsal, anal, caudal and pelvic fins mottled brown and white becoming paler at outer margins; pectorals hyaline yellowish; dental plates white or greenish.

IP: body colour brownish red, becoming paler ventrally, broad longitudinal bluish band on side; in life white spot on side at pectoral tips, this spot sometimes dark bluish; caudal fin orange-red, dorsal fin light olive-brown to dull reddish; anal and pelvic fins light reddish to pink; pectoral fins light orange-red on upper half, pale on lower; dental plates white to pinkish.

TP: body greenish overall, scales of body green posteriorly, pink anteriorly, pink colour predominating on sides and ventral region of body, green on dorsal and posterior regions; green pigment on abdominal scales may be intensified to form 2 green longitudinal lines; head, isthmus and thorax blue-green, dorsal part of head above eye and on to nape violet in life, edges of lips pink then broadly blue-green, pink more prominent on upper lip; blue-green bar on chin; upper and lower margins of orbit blue-green, these lines not extending beyond orbit; dental plates blue-green; dorsal and anal fins with blue-green base, medial salmon pink stripe beginning near origin of these fins and broadening as it passes posteriorly; broad turquoise-blue distal margin to each fin; caudal fin with broad band of salmon pink in each lobe, this colour continuous across base of fin with blue-green markings in central region, outer and distal areas of caudal fin turquoise-blue; pectoral fin with broad turquoise band on upper rays and medial pinkish zone which joins pink at fin base, ventral rays paler; pelvic fins salmon pink with broad lateral margin of turquoise.

Remarks. *Scarus forsteni* was first described by Bleeker from material collected in the Indonesian Archipelago. This species was included with *S. tricolor* in the synonymy of *S. lepidus* by Schultz (1958, 1969). Randall & Choat (1980) demonstrated that the type of *S. lepidus* was in fact *S. globiceps*, and used the next available name, *S. tricolor*. *Scarus forsteni* was included in the synonymy of this species. The junior author subsequently observed that the illustrations of IP *S. lepidus* in Schultz (1969: pl. 5 D,E) represented two different species, *S. forsteni* (5 D) and *S. tricolor* (5 E). The IP of *S. tricolor* is distinctive in life with the head, thorax and dorsum black, and black edges to the scales

in the broad blue band on the side. This persists in preservative as blackish. *Scarus tricolor* is more slender with a slightly pointed snout. Preserved IP specimens are difficult to distinguish from *S. forsteni*. TP individuals may be distinguished by the markings on the head and fins. In *S. forsteni* the upper margin of the orbit is marked by a short green bar which extends only slightly anterior to the orbit. *Scarus tricolor* has a long band through the top of the eye and a more distinctive lower orbital bar running to the upper lip. The turquoise-blue fin markings are more extensive in *S. forsteni*, covering the upper third of the pectoral fin, the outer half of the spinous dorsal and anal fin, and anterior third of the pelvic. *Scarus tricolor* has only a narrow band along the upper four rays of the pectoral with a narrow transverse blue bar at the base; the blue margins of the dorsal anal and pelvic fins are all narrower than in *S. forsteni*. Vertical fin pigmentation appears to be the best criterion for distinguishing the terminal phases of these species. The caudal fin in *S. tricolor* is strongly lunate.

The illustrations in Randall & Choat (1980: figs 11–12) are both of *S. forsteni*. Randall & Bruce (1983 pl. 5G,H) show *S. tricolor*. Both species have overlapping distributions in the western Pacific (*S. tricolor* appears to be rarer in the Pacific), the Philippines and Indonesia but only *S. tricolor* extends into the Indian Ocean. Masuda et al. (1984) show both phases of *S. forsteni*. At the time of writing only *S. forsteni* has been recorded from the Great Barrier Reef although the distribution patterns (both species are present in the Philippines and Indonesia) make it likely that increased Australian collecting will also reveal *S. tricolor*.

Callyodon elerae Jordan & Seale (1907: fig. 11) previously included in the synonymy of *S. tricolor* appears from snout and fin markings to represent TP specimen of that species. The type of *Callyodon laxtoni* was examined in the Australian Museum and is a moderately large (230 mm SL) scarid with no obvious colour pattern features remaining. There is no evidence of the blackish body shades characteristic of preserved IP *S. tricolor*. The meristic characters, body shape and emarginate caudal fin strongly suggest an IP *S. forsteni* and *C. laxtoni* is tentatively placed in the synonymy of this species.

This species was never common at any site sampled on the Great Barrier Reef. Most specimens were seen on the slopes and crests of outer-shelf reefs as solitary individuals or in pairs. It extends into deeper water (30 m). A.M. Ayling observed a few individuals at Herald Cay in the Coral Sea. Apart from an observation of pair spawning at One Tree Island nothing is known of the reproductive biology.

Scarus frenatus Lacepède

Plates 5C,D; 6J; 10H,I

Scarus frenatus Lacepède, 1802: 3, 13, pl. 1, fig. 1 (type locality, Mauritius)

Scarus sexvittatus Ruppell, 1835: 26 (type locality, Jeddah).
Callyodon upolensis Jordan & Seale, 1906: 319, fig. 59 (type locality, Apia, Western Samoa)

Callyodon vermiculatus Fowler & Bean, 1928: 472, pl. 49 (type locality, Philippine Islands)

Scarus randalli Schultz, 1958: 46, 97, pl. 19 C, text-fig. 20 (type locality, Onotoa Atoll, Gilbert Islands).

Material examined. One specimen, Heron Island, AMS I.15500-001; five specimens, One Tree Island, AMS I.17445-136, I.20572-013; one specimen, Swain Reefs, AMS IB.2741; one specimen, Great Barrier Reef, QM I.14893; one specimen, Broadhurst Reef, QM I.10355; one specimen, Coral Bay, Western Australia, WAM P.23033; three specimens (juveniles), Lizard Island, I.25799-002, I.25914-001, I.25786-002; three specimens (juveniles), Yonge Reef, AMS I.25912-001, I.25912-002; 24 specimens, Heron Island, not retained; four specimens, Lizard Island, not retained.

Diagnosis. Median predorsal scales 6–7, often two small scales anterior to first median predorsal, scales subequal, 4th or 5th largest; 3 rows of cheek scales, 6–7 scales in upper row, 6–8 scales in middle row, 2–4 scales in lower row; pectoral rays 14–15; mouth slightly inferior with lips covering most of dental plates, 0–1 canines on sides of upper dental plate; caudal truncate in smaller individuals, becoming double emarginate in larger.

Colour pattern. Juvenile: reddish brown anteriorly, darker on dorsum, caudal peduncle abruptly pale white to greenish white, thorax yellowish brown; head dark brown, dark band from snout through eye, cheek below this band pale reddish yellow; dorsal and anal fins with prominent reddish and white reticulated markings, these becoming fainter posteriorly; caudal fin whitish; pectorals hyaline brownish, pelvic light red.

IP: body brownish yellow to light red, dorsum and caudal peduncle whitish yellow; 5 dark brown stripes on side of body following centres of scale rows; fainter 6th ventral row; body scales yellowish, edged with black; head pale reddish, lighter on occiput, darker on snout, cheek and chin, dental plates white, iris orange-yellow; dorsal, anal and pelvic fins reddish; pectoral light hyaline reddish; caudal light red. Coleman (1981) has provided an excellent colour illustration of an IP *S. frenatus*.

TP: body bright green, scales of body anterior to 5th dorsal ray with orange-red vermiculations; dorsum of body and caudal peduncle abruptly lighter green; occiput and upper snout green with dense mass of orange-red vermiculations; cheek lighter green with fainter orange-red markings; tip of snout light green; upper lip orange to pink; two broad orange bands on chin, iris orange; dental plates blue-green; dorsal and anal fins with green bases, blue-green distal margins and broad medial orange-red areas marked with blue-green spots and lines; caudal fin green, basal area darker green, upper and lower lobes of caudal green with submarginal orange-red lines, central portion of fin with short orange-red lines; pectoral fins with light green upper rays, an orange-red central region, and blue-green ventral portion; pelvic fins orange-red with blue-green

anterior margin. Viewed underwater, this phase often appears as a dark green scarid with an abruptly lighter green caudal peduncle.

Remarks. *Scarus frenatus* is a wide-ranging scarid recorded from the Red Sea and extending eastwards to French Polynesia and the Pitcairn Group. In the western Pacific it ranges from the Ryukyu Islands in the north to Lord Howe Island in the south. On the Great Barrier Reef it is common on mid- and outer-shelf reefs and is moderately common on Coral Sea reefs. This species has been collected from West Australian localities. Previous records of this species from Australia have been identified as *S. sexvittatus* or *S. vermiculatus*. Surprisingly, Munro (1967) did not record it from New Guinea waters.

This species is essentially a reef-crest scarid, occurring in small groups, often associated with crevices and inlets in the reef front. It is frequently aggressive toward other species of scarids. Notes on the taxonomic status of the colour phases of this species are provided by Randall (1963) and Randall & Bruce (1983). Choat & Robertson (1975) described the sexual identity and colour phase of a large sample of this species from Heron Island. Spawning has been observed in the pair mode which may occur above a male's territory or at specific sites reached by local migration. At outer barrier reef locations larger groups (up to 40) of IP individuals may assemble for spawning. TP males do not show colour modifications while spawning. A very small proportion of primary males are present in the IP population. A moderately large scarid with terminal males reaching 330 mm S.L.

Scarus frontalis Valenciennes

Plates 5B; 9A

Scarus frontalis Valenciennes in Cuvier & Valenciennes, 1840: 280 [type locality, Oualan (= Kosrae) Caroline Islands]
Pseudoscarus jonesi Streets, 1877: 80 (type locality, Palmyra Island)

Scarus jonesi.—Schultz, 1958: 72, pl. 13 A, fig. 12.

Diagnosis. (based on central Pacific material) 4 median predorsal scales, 2 rows of cheek scales with 6 scales in each row; pectoral rays 15; mouth terminal, dental plates exposed; adults with 2–3 canines on upper dental plate; dorsal profile of snout steep, with break in contour in anterior interorbital space; caudal fin rounded in juveniles, subtruncate in subadults and emarginate to lunate in adults.

Colour pattern. This species is essentially monochromatic.

Adult colouration: body blue-green with salmon pink to purplish bar on each scale; caudal peduncle may be lighter green; head blue-green, corner of mouth salmon pink to orange; chin with broad irregular salmon pink band; broad irregular pale salmon band or blotches on throat; two narrow salmon pink postorbital bands; interorbital region with irregular broad salmon pink

band which curves on to snout; iris yellow; dorsal and anal fins orange with green markings, outer margin blue-green, the basal scaled part green; caudal fin blue-green, central unscaled region with orange longitudinal markings; pectoral fins blue-green with orange to purplish zone in upper half of fin (dorsal margin blue-green); dental plates white, often with algae growing basally.

Smaller individuals lighter green with orange scale markings not so conspicuous; caudal peduncle light yellowish green. Adult males tend to lose intensity of salmon pink or orange markings on head and body; on some large males markings may be lost, most persistent being the one at corner of mouth.

Remarks. We have no museum specimens of this parrotfish from Australia, but a colour photograph of one measuring 350 mm SL collected by the senior author at Heron Island in 1967 provides positive identification. Unfortunately, the specimen was lost after preservation and storage. An individual approximately 250 mm SL was observed and identified independently at Lizard Island in December 1983 by the senior author and D. Bellwood. A.M. Ayling (pers. comm.) observed and provided colour notes on about twelve specimens of *S. frontalis* on northern Coral Sea reefs in November 1983. This species is easily mistaken for *S. gibbus* because it is similar in colour pattern and adult males develop the same steep dorsal profile of the head as seen in *S. gibbus*.

This species has been previously identified in the literature as *Scarus jonesi* (Streets). Randall and Bruce (1983) have shown this to be a synonym of *S. frontalis*.

Scarus ghobban Forsskal

Plates 5G,H; 10D

Scarus ghobban Forsskal, 1775: 28 (type locality, Jeddah, Red Sea).

Scarus guttatus Bloch & Schneider, 1801: 294 (type locality, Indian Seas).

Scarus maculosus Lacepède, 1802: 5, 21, pl. 1, fig. 3 (type locality, Indian Ocean).

Scarus pepo J.W. Bennett, 1834: 28, fig. 28 (type locality, Ceylon).

Scarus scabriusculus Valenciennes in Cuvier & Valenciennes, 1840: 271 (type locality, Java).

Scarus lacerta Valenciennes in Cuvier & Valenciennes, 1840: 217 (type locality, Pondicherry, India).

Scarus Dussumieri Valenciennes in Cuvier & Valenciennes, 1840: 252 (type locality, Seychelles).

Hemistoma reticulata Swainson, 1839: 226 (based on *Scarus pepo* Bennett).

Scarus pyrostethus Richardson, 1846: 262 (type locality, Canton, China).

Scarus haridoides Bleeker, 1855a: 344 (type locality, Batavia and Duizend Islands).

Pseudoscarus Cantori Bleeker, 1861: 240 (type localities, Java, Sumatra, Celebes, Ambon, Timor, and Pinang).

Pseudoscarus nudirostris Alleyne & Macleay, 1877: 346, pl.xvii, fig.1 (type locality, Cape Grenville, Holotype AMS

I.16376-001).

Pseudoscarus flavipinnis De Vis, 1885: 886 (type locality, Cape York, Holotype QM I.11/83).

Pseudoscarus californiensis Pellegrin, 1901: 163 (type locality, La Paz, Gulf of California).

Scarus noyesi Heller & Snodgrass, 1903: 206, pl. 9 (type locality, Tagus Cove, Isla Isabela, Galapagos Islands).

Pseudoscarus garretti Gunther, 1909: 306, pl. 153, fig. C (type locality, Gilbert Islands).

Pseudoscarus natalensis Gilchrist & Thompson, 1909: 259 (type locality, Natal).

Scarus pyrostethus australianus Paradise in Paradise & Whitley, 1927: 103 (type locality, Cape Wessel, Northern Australia, Holotype AMS IA. 1669).

Scarus azureus Meek & Hildebrand, 1928: 742, pl. 72, fig. 1 (type locality, Panama City market, Panama).

Callyodon toshi Whitley, 1933: 61 (type locality, Southport, Queensland, Syntypes (3) QM I. 14/1634-5).

Callyodon speigleri Smith, 1956: 10, 14 (based on *Scarus dussumieri* Valenciennes, as described and illustrated by Bleeker, 1862).

Callyodon apidentatus Smith, 1956: 14, pl. 44 F (type locality, Malindi, Kenya).

Scarus fehlmanni Schultz, 1969: 24, fig. 2 (type locality, Strait of Jubal, Red Sea).

Material examined. HOLOTYPE of *Pseudoscarus flavipinnis* De Vis, QM I.11/83. HOLOTYPE of *Pseudoscarus nudirostris* Alleyne & Macleay, AMS I.16376-001. HOLOTYPE of *Scarus pyrostethus australis* Paradise & Whitley, AMS IA.1669. Eight specimens, Paisley Bay, Sydney Harbour, AMS I.18330-001, I.19103-057; one specimen, Tweed Heads, AMS I.16534-001; one specimen, Moreton Bay, QM I.6579; one specimen, Southport, QM I.1633; one specimen, Cowen, QM I.4360; three specimens, One Tree Island, AMS I. 15679-036; two specimens, Townsville, QM I.6971, I.7006; one specimen, Northwest Shelf, AMS I.22802-018; one specimen (juvenile), Lizard Island, AMS 25903-003; two specimens, Rowley Shoals, Western Australia, WAM P.25595-003; two specimens, Monte Bello Islands, WAM P.25354-041, P.25354-055; two specimens, Lacepede Island, Western Australia, WAM P.27671-015; one specimen, Rocky Bay, Western Australia, WAM P. 026615-001; two specimens, Rottne Island, WAM P.25730-001; fourteen specimens from Heron and One Tree Islands, not retained.

Diagnosis. Median predorsal scales nearly always 6, 4th scale largest; 2 small unpaired scales anterior to first scale; 3 rows of scales on cheek, upper row with 6-7 scales, rarely 5, middle row with 5-7 scales, lower row with 1-3 scales; pectoral rays 15, rarely 14 or 16; lips covering three quarters of dental plates; dental plates white to pink; large specimens with 1-3 canines on upper dental plate; posterior nostril 2-5 times larger than anterior, caudal fin emarginate in juvenile and small specimens, lunate in large specimens.

Colour pattern. Juvenile: body and median fins light grey overall; 5 diffuse blue bands on dorsum not extending to ventral mid-line; first band below 2nd and 3rd dorsal spines and last on caudal peduncle; distal margins of the dorsal, anal, outer margins of caudal, upper 2 rays of pectoral and anterior margin of pelvic fins light blue; snout and chin each with faint blue bar; blue band extending from corner of mouth a short distance diagonally downward, then curving upward to

below orbit and passing a short distance behind; short blue band through upper margin of eye; short blue band from posterior margin of orbit. In life the general impression is of a light grey scarid with slightly acute snout; blue bars appear as an intensification of blue on dorsal scales when viewed under strong lighting. Pattern of blue markings on snout and chin may be seen in some preserved specimens. In specimens from inshore areas, body colouration may be yellowish.

IP: body light yellow to orangish overall, becoming paler ventrally; individual body scales bluish, edges yellow to orange-yellow; 5 distinct irregular blue bars formed from intensification of blue on scales within bars, these usually 2 scale rows in width and distributed as follows: first beneath 2nd and 3rd dorsal spines, 2nd beneath 9th spine and 1st dorsal ray, 3rd beneath 4th and 5th dorsal rays, 4th beneath 9th and 10th dorsal rays, 5th across caudal peduncle; bars intensified on dorsum but usually not extending below body mid-line; head light yellowish; broad blue bar across snout and chin with irregular blue spots on throat; blue line from mouth to orbit and lines around orbit as in juveniles; dental plates white; usually 2 pale streaks on abdomen extending from base of pectoral to origin of anal fin; median fins blue basally, orange centrally with blue outer margins; caudal orange-yellow with broad blue upper and lower margins; pectoral pale yellow with upper margin blue; pelvic fins yellow-white with blue anterior margin. Position of blue transverse bars and blue chin and snout markings detectable in preserved specimens.

TP: dorsum of head and body green, each scale narrowly edged with salmon pink or orange; green becoming progressively reduced ventrally resulting in pinkish caste to sides and ventral region of body; cheek and operculum pale orange; chin throat and isthmus blue-green; upper lip orange with green band on snout; lower lip orange followed by green bar; chin with irregular series of green bars; green markings from mouth to orbit, and surrounding orbit as in blue markings of IP, interspaces between postorbital bars pink; median fins orange to pink with broad blue-green distal margin and green base; caudal fin green with band of salmon pink in each lobe; pectoral fins blue-green with broad orange to pink streak extending from mid-base to tips of longest rays; dark spot at upper pectoral base; pelvic fins salmon pink with broad blue anterior margin; dental plates pinkish, white at edges. Underwater, lateral pinkish area of body with green of dorsum, and green and pink head markings are striking characteristics. Green markings remain distinct when preserved. Colour illustrations of *S.ghobban* are provided by Grant (1982, IP) and Coleman (1981, IP and TP).

Remarks. *Scarus ghobban* has a very wide geographical range and occupies a variety of habitats. It occurs from the Red Sea to the Pacific coast of the tropical Americas (Randall & Bruce, 1983). In Australia *S.ghobban* extends into temperate waters and is the commonest scarid in museum collections from Sydney

Harbour on the east coast and from Rottne Island on the west coast. It is also characteristic of a variety of tropical non-reef environments, including shallow mangrove and seagrass areas (Blaber et al., 1985), as well as deeper water habitats sampled by trawling. *Scarus ghobban* is the only scarid regularly collected during trawling operations on the Australian north-west shelf (J.Paxton, pers. comm.).

Observations on northern reefs by the senior author suggest that this species differs from most congeners in that it is not typically a reef associated scarid. At Lizard Island large individuals were uncommon on reefs, which were used mainly as spawning sites. After spawning on deep reef fronts, large TP and IP individuals were observed to move back out over surrounding seagrass and algal beds in water greater than 30m depth.

Probably because of its wide-ranging distribution and occurrence in inshore habitats this species is prominently represented in early Australian collections of fishes. This has resulted in a complex synonymy for *S.ghobban*. *Pseudoscarus nudirostris* (Alleyne & Macleay) and *P.flavipinnis* (De Vis) were not assigned identities by Schultz (1969) in his review. Types of both species are lodged in the Queensland and Australian Museum respectively: both proved to be *Scarus ghobban*. Examination of the type of *Scarus pyrrhostethus australianus* (Paradice) confirmed the identification reported by Randall & Bruce (1983) as *S.ghobban*.

The identity of *Callyodon toshi* Whitley is more problematical. Schultz (1958) initially concluded that *C.toshi* was unidentifiable but later (Schultz, 1969) included it erroneously in the synonymy of *Scarus harid*. Tosh (1903) provided a brief description and a figure of a scarid from Southport, Queensland identified as *Heteroscarus* sp. This material was apparently deposited in the Queensland Museum and later identified as *Callyodon cyanotaenia* (Bleeker) by Ogilby (1915). He noted that there were three examples of this species in the Queensland Museum collected by Tosh at Southport. Whitley (1933), after comparing the figure in Tosh (1903) with Bleeker's description of *Scarus cyanotaenia*, concluded that Tosh had figured an undescribed species and proposed the name *Scarus toshi*. No type of *Scarus toshi* was designated. Three small scarids (82–85 mm SL) collected by Tosh at Southport in 1901, deposited in the Queensland Museum and later registered (I.14/1634-5, 1913) and identified by Ogilby (1915) as *Callyodon cyanotaenia*, were examined by the senior author in the Queensland Museum. All proved to be juveniles of *S.ghobban*. In addition, the illustration of *Heteroscarus* sp. in Tosh (1903) strongly suggests this species. Other examples of scarids in the Queensland Museum identified as *S.cyanotaenia* also proved to be *S.ghobban*. Material in the Australian Museum identified as *S.toshi* proved to be *S.ghobban* or in the case of Whitley (1966: fig.3), *Scarus psittacus*. No candidate for the type of *Scarus toshi* could be located in the Australian Museum. The specimens collected by Tosh at Southport and later deposited in the Queensland Museum must represent the

material on which the description of *Heteroscarus* sp. was based, and are therefore syntypes of *Scarus toshi* Whitley.

Scarus gibbus Rüppell

Plates 2C,D; 6C; 7A,B.

Scarus gibbus Rüppell, 1828: 81, pl.20, fig. 2 (type locality, Mohila, Red Sea).

Scarus microrhinos Bleeker, 1854b: 200 (type locality, Batavia).

Scarus strongylocephalus Bleeker, 1854d: 439 (type locality, Batavia).

Pseudoscarus microcheilos Bleeker, 1861: 231 (type locality, Java).

Callyodon ultramarinus Jordan & Seale in Seale, 1906: 63 (type locality, Samoa).

Material examined. One specimen, Heron Island, AMS I.15504-001; two specimens, Lizard Island, AMS I.19445-016, I.19464-005; three specimens, Swain Reefs, QM I.12732, I.19146, I.16005; one specimen, Rowley Shoals, WAM P.27654-030; four specimens (juveniles), Lizard Island, AMS I.25782-003, I.25905-001, I.25909-002, I.25913-001; 25 specimens Heron Island & One Tree Island not retained.

Diagnosis. Median predorsal scales 4; scale rows on cheek 3, upper and middle rows 5–7 scales, lower row with 3–8 scales (usually 5–6); pectoral rays 16; caudal fin varying from emarginate in subadults to highly lunate in adults; dental plates broadly exposed, 1–2 canines on upper dental plate, none on lower; small adults develop prominence on forehead at level of eye; with growth this develops into a vertical profile.

Colour pattern. Juvenile (20–80 mm): body dark brown to black with 3 longitudinal whitish stripes, first from eye to end of dorsal fin, 2nd from below eye across cheek to base of caudal fin, 3rd across lower margin of cheek, through pectoral base to posterior end of anal fin; dorsal, anal and caudal fins dark brown; posterior margin of caudal fin whitish; pectoral fins hyaline with yellowish base; dental plates whitish.

Between 80 and 150 mm most Great Barrier Reef juveniles uniform blackish brown with whitish dental plates and pale crescentic region on caudal fin.

Green phase (150–280 mm): body dark green with narrow brown to orange bar on each dorsal scale; abdomen and thorax paler (on southern reefs 2 darker green abdominal bars may be present); caudal peduncle light greenish, occiput light greenish, often with darker green flecks; snout and sides of head below eye brownish to dark purple; eye rim blue-green, often with two short postorbital bars, upper lip green, lower lip and chin with extensive green blotch which extends into broad irregular green band passing horizontally across cheek and continuing dorsally on margin of opercular membrane; cheek below this line paler; dorsal and anal fins reddish brown with posterior medial light green line, caudal greenish with vertical reddish brown bar and darker posterior margin; pectorals greenish; pelvics reddish brown with lighter margin; dental plates whitish green, becoming darker with increase in size.

Green Phase (> 300 mm): body light green to bluish green with narrow orange to rose bar on each scale; body becoming pale bluish green on abdomen and thorax; caudal peduncle lighter green; sides of body light pinkish; occiput blue-green, sides of head and snout purple, this becoming strongly developed in large male specimens; eye rimmed with blue-green; upper lip bounded by thin blue-green line, lower lip and chin with large blue-green blotch which extends horizontally across cheek as a characteristic irregular green band which continues dorsoposteriorly on opercular membrane; cheek below this line abruptly pale yellowish; dorsal and anal fins orange with blue-green basal and distal margins; anal fin with medial green band of variable length in soft portion; caudal fin green to blue-green with broad zone of purplish to dull rose in each lobe connecting across basal unscaled portion with markings of same colour; pectoral fins purplish green becoming hyaline distally and ventrally, upper edge blue-green; pelvic fins orange to pink, margins broadly blue-green; dental plates green, whitish at margins, iris blue-green. In alcohol-preserved specimens the green pigment, including horizontal cheek band, remains prominent.

These descriptions refer to Great Barrier Reef material. A preserved green-phase specimen from the West Australian museum collection, (P.27654-030; Rowley Shoals) displayed green pigmentation on head region, including horizontal cheek band similar to Great Barrier Reef specimens.

In life, colouration of snout and sides of head in large individuals may vary from purple to light brownish quite rapidly; in Great Barrier Reef specimens there is no evidence of the salmon pink margin to the upper lip as seen in central Pacific specimens.

Red phase (observed developing at approximately 100 mm): dorsum of head and body to mid-line light red, below this light yellowish; cheek below line from corner of mouth to pectoral base abruptly paler; upper lip with distinct yellow margin, lower lip with paler yellow margin; basic head colouration pattern corresponding to that seen in the green phase; dorsal, anal, caudal and pectoral fins uniform pale yellowish, in large specimens outer margins of dorsal and anal fins greenish; pelvics yellow with greenish lateral margin; dental plates green; iris yellow. Alcohol-preserved specimens retain reddish pigment and are readily distinguished from green-phase individuals.

Remarks. Schultz (1958) erroneously placed *S. gibbus* in the synonymy of *Bolbometapon muricatum*; he also considered *S. strongylocephalus* and *S. microcheilus* as junior synonyms of *S. microrhinos* and thus included western Indian Ocean, Indo-West and central Pacific populations under the name *S. microrhinos*.

Smith (1959) clarified the status of *S. gibbus* and recognized it as one of three distinct species in the 'gibbus' complex. He distinguished these from other scarinine parrotfishes with the erection of the genus *Chlorurus*. *Scarus gibbus* and *S. strongylocephalus* were identified as Red Sea and Indian Ocean species

respectively, and *S. microrhinos* as western and central Pacific. Smith considered that the species described by Bleeker as *S. microcheilus* was the female and junior synonym of *S. strongylocephalus*.

Schultz (1969) reviewed a number of problems of scarid taxonomy including the species of the '*gibbus*' complex. After comparing structural, meristic and colouration characteristics among *S. gibbus*, *S. microrhinos* and *S. strongylocephalus* he placed all within the synonymy of *S. gibbus*. He also saw no justification for separate generic status for *S. gibbus*. The genus *Chlorurus* was therefore placed in the synonymy of *Scarus*.

Scarus gibbus is a member of a complex of large, deep-bodied scarids with four median predorsal scales, 16 pectoral rays and characterised by a highly convex snout profile, exposed dental plates, and lunate caudal fins. This complex has a broad geographical distribution, extending from the Red Sea, through the Indian Ocean, the Indonesian Archipelago to the western and central Pacific. The recent taxonomic history of this complex is confused. At present a number of populations which may be differentiated on the basis of colour pattern are combined within a single taxon, *Scarus gibbus* Rüppell, following Schultz (1969).

Three nominal species are of interest here: *Scarus gibbus* Rüppell, 1828, *Scarus strongylocephalus* Bleeker, 1854, and *Scarus microrhinos* Bleeker, 1854. The geographical distribution of this complex is similar to that seen in other scarid species; there are distinctive populations in the Red Sea, the Indian Ocean, and the central and west Pacific. The Red Sea populations (from which the type of *S. gibbus* was collected) are distinct from those of the central and west Pacific in several features of colouration (Smith, 1959; Randall & Choat, 1980; Randall & Bruce, 1983). Those members of the *S. gibbus* complex occurring in the western and central Pacific have been identified in earlier works as *S. microrhinos*. The Indian Ocean populations show similarities with the scarid described by Bleeker as *S. strongylocephalus*.

Information available to date does not allow a formal statement about the biological status of the three populations of *Scarus gibbus*. Although the Red Sea and Pacific populations are distinct in terms of colour, the Indian Ocean population shows a considerable degree of overlap with the others. In addition, the unusual pattern of colour phases seen in some populations of *S. gibbus* (Randall & Choat, 1980) suggests the relationship between colour, sexual identity and reproductive behaviour is likely to be complex and possibly different from other scarids. Until more material is available, especially from the Indian Ocean; and there is a better understanding of the reproductive biology of *S. gibbus*, we will follow other workers and provisionally recognize a single taxon, *S. gibbus*.

Scarus gibbus has a wide distribution in Australian waters, being found the entire length of the Great Barrier Reef and extending into Western Australian waters. A juvenile was observed and photographed in

a subtropical reef environment in Western Australia (Rottnest Island; B Hutchins pers. comm.). It occupies a variety of habitats, being recorded from inshore reefs to the Coral Sea. It is a conspicuous member of the Great Barrier Reef scarid fauna, being characteristic of reef crests and adjacent reef flats where it often grazes in small schools. This is one of the larger scarids with a maximum size from Australian collections of 421 mm SL. A major source of interest in *S. gibbus* is the atypical pattern of colour variation with red and green phases occupying a similar size range rather than the usual sequential size-related patterns of colour change. Many individuals in the green colour phase were found to be females. Fourteen green phase specimens from Heron Island, ranging from 120 to 400 mm SL, which were examined histologically proved to be females. In almost all other scarids, individuals with predominantly green colouration have been found to be males. The status of the red phase is discussed by Randall & Choat (1980).

Scarus globiceps Valenciennes

Plates 4E,F; 11B,C

Scarus globiceps Valenciennes in Cuvier & Valenciennes, 1840: 242 (type locality, Tahiti).

Scarus lepidus Jenyns, 1842: 108 (type locality, Tahiti).

Pseudoscarus spilonotus Kner, 1868: 352, pl.9, fig.26 (type locality, Fiji Islands).

? *Pseudoscarus strigipinnis* De Vis, 1885: 886 (type locality, Cardwell, Queensland, Holotype QM I.963).

Pseudoscarus fuscus De Vis, 1885: 887 (type locality, Barrier Reef, Holotype QM I.41).

Scarus pronus Fowler, 1899: 490, pl.18, fig.3 (type locality, Caroline Atoll).

Material examined. HOLOTYPE of *Pseudoscarus fuscus* De Vis, QM I.41. HOLOTYPE of *Pseudoscarus strigipinnis* De Vis, QM I.963. Ten specimens, One Tree Island, AMS I.15686-027, I.17445-137, I.19445-014, I.20464-016; one specimen, Lord Howe Island, AMS I.17357-018; one specimen, Heron Island, QM I.11964; two specimens, Hopkinson Reef, QM I.6007, I.6008; one specimen, Trunk Reef, QM I.6622; one specimen, Rowley Shoals, Western Australia, WAM P.27667-014; 70 specimens Heron and Wistari Reefs, not retained; nine specimens, One Tree Island, not retained; nine specimens, Lizard Island, not retained.

Diagnosis. Median predorsal scales 5–6, rarely 7, subequal, 3rd or 4th scale largest; in specimens with 5 scales, usually a small pair of scales anterior to first; 3 rows of cheek scales, upper row with 5–7 scales, middle row with 6–8, rarely 9 scales, lower row with 1–4 scales; pectoral rays 14; lips covering or nearly covering dental plates; dental plates white; IP fish with no canines on dental plates, TP with 1–2 canines on upper and lower dental plates (small TP individuals may lack canines); caudal fin truncate in IP, double emarginate in TP, in some individuals lobes produced to form lunate caudal fin; dorsal profile of head of TP fish with slight hump in upper interorbital space.

Colour pattern. IP: body colour varies from light grey to dark brown overall, becoming lighter ventrally; 3 pale

lines on abdomen following centres of scale rows, upper 2 most prominent; dorsal fin brownish grey with blue-grey distal margin; anal and pelvic fins reddish brown; caudal fin brownish, distal region paler; pectoral fin brownish becoming paler ventrally, dusky spot at pectoral base; upper region of iris blue in life. In feeding schools, especially in shallow water, body usually light grey overall; in smaller groups or solitary, especially in deeper water, body dark brown or grey with reddish fins, with prominent pale margin to caudal fin. Some individuals with 6–7 indistinct pale blotches along dorsum (Fig.5). Dark body colouration characteristic of individuals prior to group spawning. During group spawning, primary males dusky grey with grey horizontal interorbital band, corresponding to blue-green band in the TP; females either uniform dusky grey or with indistinct dusky transverse bands. Juvenile specimens (smaller than 25 mm) often with series of dark longitudinal bands. On preservation, body and fins uniform greyish brown with the pale longitudinal abdominal bands often visible.

TP: green overall; body scales each with pink to orange bar; abdominal scales with coalescent green pigment forming 3 longitudinal bands along the scale centres; thorax and posterior caudal peduncle uniform green; numerous small green spots on head and anterodorsal region of body; head with narrow green bands radiating from orbit (except ventrally); horizontal pink band passing anteriorly from eye across front of snout, this band extending posterior to orbit across operculum; head below band light green, especially on cheek; front of snout and upper lip blue-green; dorsal and anal fins with broad blue-green basal band, broad median band of orange, and blue border; soft dorsal fin with median row of green spots; small dark spot on dorsal fin near base of 4th dorsal spine; caudal fin green, usually with submarginal streak of orange on each lobe; pectoral fins blue-green, darker dorsally, longitudinal orange streak along upper third of fin, dark spot on upper pectoral base; pelvic fins salmon pink with blue lateral border. Green markings and position of horizontal interorbital band prominent in preserved specimens.

Remarks. De Vis (1885) described *Pseudoscarus strigipinnis* from a fish 6 inches in total length from Cardwell, Queensland. He reported it as having 3 rows of scales on the cheeks, the lowest of 5 scales, 14 pectoral rays, and a truncate caudal fin. He provided the following colour notes: 'Grey clouded with darker grey. Fins black, the caudal with alternating white longitudinal stripes equally the black intervals in breadth. Dorsal, anal and pectoral, with irregular white lines and streaks in the direction of the rays. All the white streaks appearing as if laid on with pigment.' The holotype is in the Queensland Museum (QM I.963, 127 mm SL). It is stuffed, uniform dark brown and in poor condition. We can confirm that there are 14 pectoral rays. We count 4 scales in the third (lowermost) row on the cheek on the right side, and there appear to have

been three on the left side. There are 6 median predorsal scales (though damage to the nape does not rule out the possibility of a seventh scale). Of the species of *Scarus* which are known to occur in Queensland waters, there are seven which share these meristic characters: *S.globiceps*, *S.rivulatus*, *S.oviceps*, *S.dimidiatus*, *S.forsteni*, *S.frenatus* and *S.niger*. None at any size have the colour pattern as described by De Vis. We tentatively place *P.strigipinnis* in the synonymy of *S.globiceps*. Our observations suggest that both *S.rivulatus* and *S.globiceps* might be found in the Cardwell area. The other species are more characteristic of outer reef areas. The cheek scale counts are consistent with *S.globiceps*.

The type of *Pseudoscarus fuscus* De Vis (1885) (QM I.41, 208 mm SL) is also present as a stuffed and mounted specimen in the Queensland Museum. It is now uniform dark brown with some disintegration of the caudal fin but all scales are detectable. There is a nuchal hump. De Vis recorded 2 rows of scales on the cheek but the type has 3 rows with 2 scales in the third row. The type has 6 median predorsal scales and 14 pectoral rays; there are two canines on the lower dental plate. This combination of characters (especially the canine teeth) suggests *S.globiceps* TP. A TP individual correctly identified as *S.globiceps* in the Queensland Museum (I. 11964) also shows a similar nuchal hump. *Pseudoscarus fuscus* is placed in the synonymy of *S.globiceps*. The colour note of De Vis, 'uniform brownish olive' probably refers to the preserved condition.

Grant (1982) provided colour photos of *S.globiceps* identified as the male and female colour phases. Both are of TP males.

IP individuals have proved difficult to differentiate from those of *S.rivulatus* during underwater observation and in preserved collections (Randall & Choat, 1980). Additional material to assist in differentiation is discussed in the Remarks section of *S.rivulatus*.

Scarus globiceps is a widespread species in the Indian Ocean and tropical western and central Pacific. It is common on reef crests and fronts in mid- and outer-shelf reefs in the Great Barrier Reef region, and is present on western Australian reefs. Museum and observational records suggests that it does not occur in inshore non-reef areas or extend into temperate environments. *Scarus globiceps* consistently assembles in large numbers (20–30 per spawning run) for group spawnings, such groups being characterised by a high proportion of primary males (Choat & Robertson, 1975; Randall & Choat, 1980). Sampling of *S.globiceps* populations in non-spawning situations has revealed a consistently high proportion of primary males in the initial colour phase. This species is a relatively small scarid, with TP males not usually exceeding 250 mm SL.

Scarus longipinnis Randall & Choat Plates 3E,F; 7J

Scarus longipinnis Randall & Choat, 1980: 414, figs 32, 33 (type locality, Pitcairn Island).

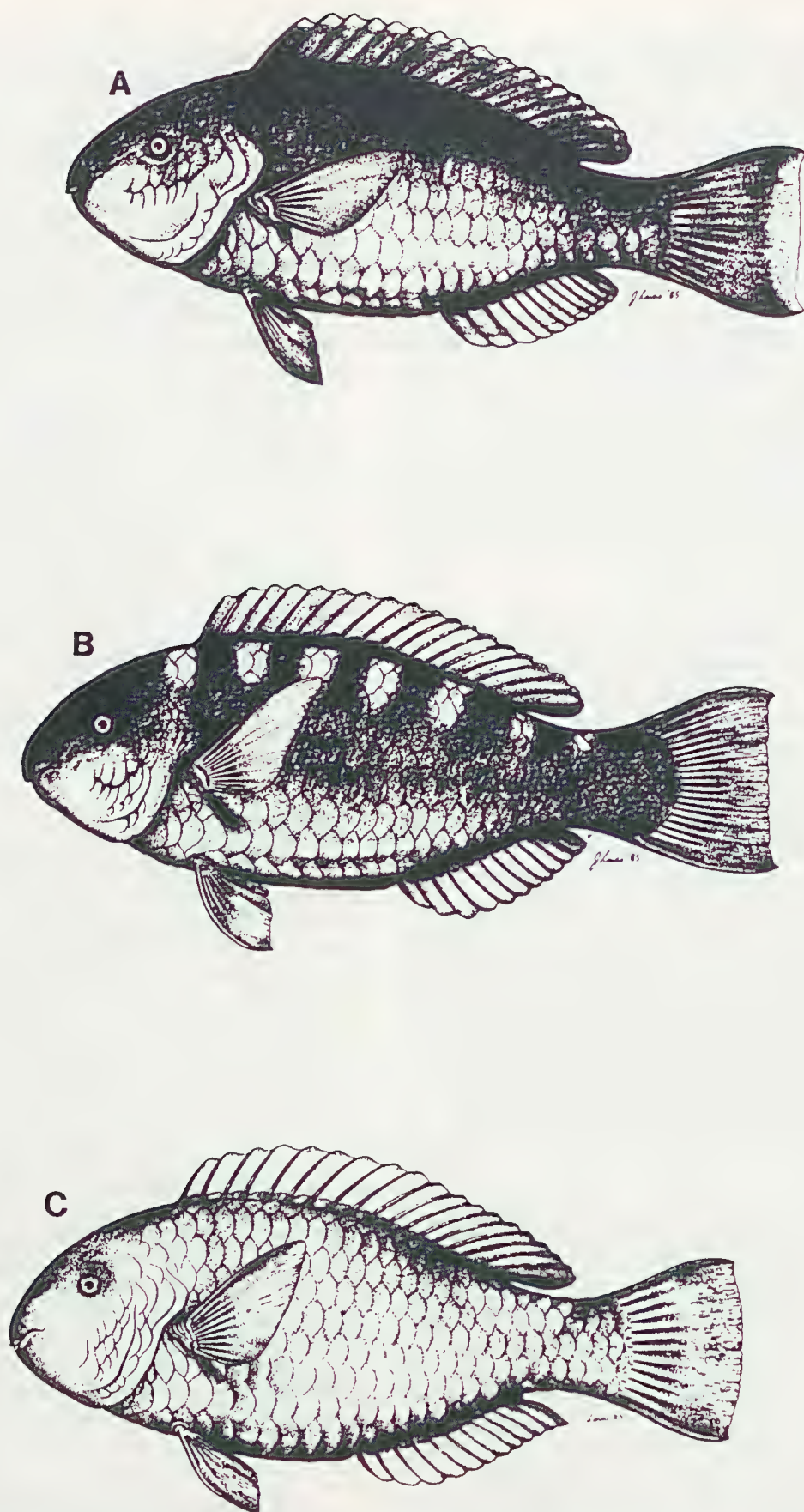


Fig. 5. Diagrams of small IP individuals of A, *S. psittacus* B, *S. globiceps* and C, *S. rivulatus* showing the main criteria for separating these species in the field. Each individual is approximately 120 mm SL and was collected at Lizard Island. See text under the species description of *S. rivulatus* for details.

Material examined. Three specimens, Heron Island, AMS I.21379-001, I.21379-002, I.21279-003; two specimens, One Tree Island, AMS I.17929-013, BPBM 14381; one specimen, Escape Reef, AMS I.22596-002; one specimen, Carter Reef, AMS I.25784-001; one specimen (juvenile), Lizard Island, AMS I.25789-001; one specimen, Kenn Reef, Coral Sea, AMS IB.4995.

Diagnosis. Median predorsal scales 4 (occasionally 3), subequal; 3 rows of scales on cheek, upper row with 5-7 scales, middle row with 5-7 scales, lower row with 1-3 (usually 2) scales; pectoral rays 14; mouth nearly terminal, lips covering the dental plates, adults with 1-2 canines on upper dental plates; body deeper than average for the genus with depth about 2.5 in SL; dorsal fin elevated, longest dorsal ray 1.7-2.1 in head; pelvic fins long for genus, longest ray in adults 1.2-1.5 in head; caudal fin rounded in juveniles, slightly emarginate to very lunate in adults.

Colour pattern. IP: yellowish brown shading to light reddish brown ventrally; 3 bluish stripes on thorax and abdomen; posterior region of body with 5 dusky bars which vary in intensity, first at level of pectoral tips, last on base of caudal peduncle; body between first dusky bar and operculum paler; bluish bar crossing cheek diagonally from lower margin of orbit to posterior opercular margin, faint dusky bar above this, bluish spot on snout below nostrils; slender anterior projection of this spot reaching upper lip, bluish band arching downward behind mouth, running posteriorly along lower edge of operculum, bluish blotch above each eye, iris brownish orange; occiput brownish, upper and lower lips brownish red; dorsal fin yellow-brown anteriorly with narrow blue-grey edge, becoming darker posteriorly, in larger specimens purple area basally on each interradi al membrane posterior to 7th spine; anal fin with outer third green, basal two thirds orange-brown with greenish spot at base behind each ray; caudal fin brownish orange with median posterior crescent of yellow-green, extreme posterior margin dusky; pectoral fins light yellow with greenish bar at base; pelvic fins light reddish with light blue lateral edge.

Viewed underwater IP individuals give impression of dark brown posterior body with faint dusky bars, pale anterior body region, lateral and ventral regions of head lighter with bluish lines of head discernable, and the posterior margin of caudal fin abruptly yellowish. In smaller specimens, bluish head lines appear dusky.

TP: body orange-brown, body scales with vertical green bar; 5 green bars on body, first beneath base of 6th dorsal spine, 4th at rear base of dorsal fin, last on caudal peduncle, curved 6th green bar on scaled base of caudal fin; first green bar of body continuous with band of green 2 scale rows in width on back passing to nape; 2 green stripes ventrally on body and a third on the lower abdomen; dark green band passing from upper interorbital to front of eye where briefly interrupted, thence to corner of mouth where a branch extends on to upper lip and a broader lower branch on to chin; lower part of head greenish, cheeks orange-brown; dark green band from lower edge of eye to upper

pectoral base and another more diffuse one above it from centre of eye, broadening over upper opercle, lower lip with green line; dorsal fin yellowish red anteriorly, edged in blue, first interspinous membrane darker, fin becoming broadly yellowish green on outer part and purplish in lower portion posterior to 7th dorsal spine; anal fin with broad outer margin of blue, middle pinkish zone and basal zone of greenish spots, one on each interradi al membrane; unscaled part of caudal fin pinkish across base and on to lobes, edges of lobes dark green, posterior central region of fin yellow-green with dark green edges; pectoral fins light orange-yellow, becoming green and lavender at base; pelvic fins greenish yellow with broad blue lateral edge. Underwater, orange areas of head and body may appear pinkish or lavender, contrasting strongly with the green bars. On preservation, green cheek bar remains as dusky line after most other markings have faded.

Remarks. This scarid is recognized by its deep body, elevated dorsal and long pelvic fins. On the Great Barrier Reef this species is generally confined to deeper waters off reef fronts. On the southern reefs such as the Capricorn-Bunker Group this species may be encountered in 10-15 m depth, but on northern reefs it is rarer and characteristic of deeper areas (20-30m) on outer-reef fronts. It is generally solitary or occurs in small groups.

The abundance of this species dramatically increases on Coral Sea reefs. Here it is consistently the most abundant scarid and may congregate in large groups. A.M. Ayling found this species to be an order of magnitude more abundant than other scarids on two cays of Lihou Reef. D. Williams also recorded high abundances at Flinders Reefs and Middleton Reef. This species has also been observed to occur at high densities on the eastern-most reefs of the Swain Group (A.M. Ayling pers. comm.). Other than the identification of protogyny and the observation of pair spawning we have no information on the reproductive biology.

Scarus niger Forsskal, 1775

Plates 5A; 6G; 10J; 11A

- Scarus niger* Forsskal, 1775: x, 28 (type locality, Red Sea).
Scarus nuchipunctatus Valenciennes in Cuvier & Valenciennes, 1840: 224 (type locality, Dutch East Indies).
Scarus limbatus Valenciennes in Cuvier & Valenciennes, 1840: 271 (type locality, Macao).
Pseudoscarus flavomarginatus Kner, 1866: 262, pl. 10, fig. 2 (type locality, Java).
Pseudoscarus madagascariensis Steindachner, 1888: 61, pl. 2, fig. 1 (type locality, Madagascar).
Callyodon maoricus Jordan & Seale, 1906: 328, pl. 48, fig. 3 (type locality, Pago Pago, Samoa).
Pseudoscarus godeffroyi Gunther, 1909: 326, pl. 159 (type locality, Society Islands).
Callyodon lineolabatus Fowler & Bean, 1928: 257, pl. 47 (type locality, Butauanan Island, Philippine Islands).

Material examined. One specimen, Heron Island, AMS I.15477-001; two specimens, One Tree Island, AMS

I.15679-038, I.20680-005; one specimen, Big Broadhurst Reef, QM I.10355; two specimens, Escape Reef, AMS I.22581-029, I.22586-041; three specimens, Lizard Island, AMS I.19464-006; three specimens (juveniles), Lizard Island, AMS I.25907-001, I.25914-002, I.25909-004; two specimens (juveniles), Yonge Reef, AMS I.25912-004; three specimens, Raine Island, AMS I.20775-009, I.20775-010; seven specimens, Heron Island, not retained; four specimens, Lizard Island, not retained.

Diagnosis. Median predorsal scales 6–7, subequal (first may be small and partially embedded), fourth usually largest; 3 rows of scales on cheek, 6–7 scales in upper row, 6–9 scales in middle row, 3–5 scales in lower row; pectoral rays 14, occasionally 15; dental plates largely covered by lips, upper dental plate with 0–2 canines on each side; caudal fin in small individuals rounded, in larger individuals lobes become extended, dorsal more than ventral, in large males fin double emarginate with extended lobes; penultimate anal ray prolonged in large males.

Colour pattern. In the western and central Pacific there is no obvious sexual differentiation in colour patterns into an initial and terminal phase. Juveniles are distinct.

Juvenile: body dark brown to blackish with paler caudal peduncle, white in very small specimens to reddish brown in larger, dark spot on dorsal and ventral aspects of caudal peduncle; series of fine bluish white dots on body, snout pale brown; dorsal fin pale brown with darker distal margin, anal fin brownish, caudal fin pale, pectorals light yellow, pelvics dark brown.

Adult: body dark blackish brown; scales in mid-region of body each with 3–4 darker spots on posterior region, these scales with greenish caste which fades rapidly with removal from water, green spot with darker margin on body adjacent to upper opercular membrane, snout reddish with green band crossing snout above upper lip, chin with 2 green bars; greenish band from corner of mouth to lower margin of orbit, 2 short green postorbital bands, sides of head with darker dots and reticulated markings; subopercular area often with greenish dots, dental plates blue-green; dorsal and anal fins reddish brown, distal margins blue-green; caudal fin brownish, upper and lower margins blue-green, then submarginally reddish brown, posterior margin narrowly greenish; upper part of pectoral fins light brown, dorsal-most ray slightly darker, lower rays hyaline dark brown; pelvic fins brownish, spine and anterior rays blue-green. Larger males, body colouration becomes progressively darker purplish green, black spots on body scales and head less prominent. A colour illustration of a large male *S. niger* is provided by Coleman (1981).

Remarks. *Scarus niger* has a similar distribution pattern to *S. frenatus*, ranging from the Red Sea to the central Pacific. Western and central Pacific populations of *S. niger* have mainly secondary males (Choat & Robertson, 1975) but do not have the characteristic IP and TP colours usually associated with this pattern of sexual ontogeny. In Red Sea and western Indian Ocean

populations there are initial and terminal phases although they are not as distinctive as in most other scarid species. TP individuals are very similar to the large males described here, the major distinction being a red pectoral fin in western Indian Ocean populations. Details of these colour phases are provided by Randall & Bruce (1983). Gunther (1909) has provided an excellent illustration of *Pseudoscarus godeffroyi* (type locality Society Islands). This is clearly *S. niger* and is included above in the synonymy of this species.

Scarus niger is widely distributed on mid, outer and Coral Sea reefs of the Great Barrier Reef. It is usually found on reef front habitats in small groups, a characteristic it shares with *S. frenatus*. However it occupies a greater range of habitat types than *S. frenatus* and typically occurs in slightly deeper water. It has not been recorded from Western Australia although it occurs on northern Australian reefs (B. Russell, pers. comm.).

Large males are often observed on reef fronts swimming rapidly with the caudal fin elevated, the elongate rays of the anal fin produced downward and the upper lip curled back to expose the dental plates. These characteristics are associated with reproductive behaviour prior to pair spawning. This species defends specific feeding sites against other scarids.

Scarus niger may be the only monandric scarid on the Great Barrier Reef. Histological studies have revealed no primary males (Choat & Robertson, 1975) although additional work is required to confirm this. Recent observations demonstrate that this species makes local migrations to specific spawning sites and is not restricted to male territorial areas when spawning, as suggested by Choat & Robertson (1975). It is a moderate-sized scarid, with large males reaching 350 mm SL.

Scaris oviceps Valenciennes

Plates 4G,H; 10G

Scarus oviceps Valenciennes in Cuvier & Valenciennes, 1840: 244 (type locality, Tahiti)

Pseudoscarus zonatus Macleay, 1883: 591 (type locality, New Guinea)

Callyodon lazulinus Jordan & Seale, 1906: 333, fig. 65 (type locality, Samoa)

Material examined. HOLOTYPE of *Pseudoscarus zonatus*, AMS I.16379-001, New Guinea. One specimen, Heron Island, AMS I.15492-001; one specimen, Cairns, QM I.19098; one specimen, Rowley Shoals, Western Australia, WAM P.27667-013; one specimen, New Guinea, QM I.11449; one specimen (juvenile), Lizard Island, AMS I.25794-002; two specimens, Heron Island, not retained; five specimens, Lizard Island, not retained.

Diagnosis. Median predorsal scales 6; 3 rows of scales on cheek, upper row with 6–7 scales, middle row with 6–9 scales, lower row with 2–3 scales; 14 pectoral rays; caudal fin lunate in both IP and TP individuals; lips

covering teeth; no canine teeth on dental plates.

Colour pattern. Juvenile: body pale yellow, upper snout, occiput and dorsum to end of spinous dorsal dark, 2 pale bars dividing dark dorsal pigmentation, dark colouration not extending below mid-line of body; characteristic darker band from snout, through eye, to beyond opercular membrane, cheek below this abruptly paler; fins hyaline yellow (Plate 10G).

IP: lower body yellowish brown, becoming lighter ventrally; scales may be edged with grey; upper body darker, becoming less pronounced posteriorly; snout, occiput and dorsum to level of 8th dorsal spine dark brown to black; dorsum with 2 yellow saddles, 1st between 7th spine and first dorsal ray, 2nd between 6th and 7th dorsal rays, these pale saddles diagonal and pointing forward; dorsal fin dusky, distal margin reddish brown; anal and pelvic fins reddish yellow; caudal hyaline light brown; pectoral hyaline yellowish, upper rays darker; dental plates white.

TP: body blue-green with anterior portion of each scale pinkish, body colouration becoming paler ventrally; head above lower edge of eye and body above pectoral fin and anterior to 8th dorsal spine abruptly dark purplish; cheek lighter blue-green, separated from darker region of head by greenish band running from snout, below eye to opercular margin; lips blue-green and a blue-green bar on chin; dorsal and anal fins greenish with narrow blue margins; caudal fin greenish with posterior blue margin; pectorals greenish, becoming lighter ventrally, upper rays yellowish green; pelvics blue-green, spine and anterior rays darker; dental plates green.

Remarks. *Scarus oviceps* is a member of a complex of closely related species including *S.scaber* and *S.dimidiatus*. These are characterised by an IP colour pattern comprising diagonal dark and yellow saddles on the dorsum. *Scarus oviceps* and *S.dimidiatus* co-occur on the Great Barrier Reef and in the western Pacific, while *S.scaber* is restricted to the western Indian Ocean. A point of interest is the relationship between similarity of colour patterns and geographic distribution. The IP of *S.scaber* is almost identical to that of *S.dimidiatus*; while the TP of *S.viceps* is very similar to that of *S.scaber* (Randall & Bruce, 1983). The strongest similarities occur in geographically separated members of the complex. The marked similarities between the terminal phases of *S.viceps* and *S.scaber* and resultant taxonomic confusion are discussed by Randall & Choat (1980).

Scarus oviceps is widely distributed on the Great Barrier Reef, occurring on mid- and outer-shelf reefs. Specimens have also been recorded from Western Australia. It tends to be solitary or occurs in small groups in more sheltered habitats, often amongst large *Acropora* growths. Care should be taken with field identifications of the terminal phase which may be confused with *S.forsteni*. This is a moderately sized scarid, with terminal males reaching 300 mm SL.

Scarus psittacus Forsskal
Plates 2E,F; 6D; 8A,B,C,D.

- Scarus psittacus* Forsskal, 1775:29 (type locality, Jeddah).
Scarus venosus Valenciennes in Cuvier & Valenciennes, 1840: 212 (type locality, Reunion).
Scarus taeniurus Valenciennes in Cuvier & Valenciennes, 1840: 257 (type locality, Mauritius).
Scarus hertit Ehrenberg in Cuvier & Valenciennes, 1840: 215 (type locality, Red Sea).
Scarus forsteri Valenciennes in Cuvier & Valenciennes, 1840: 275 (type locality, Tahiti).
Pseudoscarus Filholi Sauvage, 1880: 225 (type locality, Fiji Islands).
Pseudoscarus labiosus MacLeay, 1883: 585, (type locality, Port Moresby).
Scarus gilberti Jenkins, 1900: 59, fig. 17 (type locality, Hawaiian Islands).
Scarus jenkinsi Jordan & Evermann, 1903: 195 (type locality, Honolulu).

Material examined. NEOTYPE of *Scarus psittacus*; Red Sea, BPBM 19789; HOLOTYPE of *Pseudoscarus labiosus*, New Guinea, AMS I.16376-001. Three specimens, Heron Island, AMS I.154800-001; four specimens, One Tree Island, AMS I.15686-027, I.1717445-131, I.20479-018; one specimen, Lord Howe Island, AMS I.17388-004; four specimens, Gillett Cay, Swain Reefs, AMS IB.6082, IB.6084, IB.6085, IB.6086; ten specimens, Lizard Island, AMS I.18805-019, I.19445-014, I.194455-016, I.19464-008, I.19469-009, I.19482-105, I.21343-014; one specimen, Rowley Shoals, Western Australia, WAM P.27658-035; 45 specimens, Heron Island, not retained; eighteen specimens, Lizard Island, not retained.

Diagnosis. Median predorsal scales 4, subequal (largest scale 1st in juveniles, 2nd in adults); no anterior paired scales; 2 rows of cheek scales; upper row 5-7 scales, lower row 4-7 scales; pectoral rays 14, rarely 15; lips covering dental plates; 0-2 canine teeth on upper and lower dental plates; large TP males with 2 upper and 1 lower tooth; large IP with 1 upper tooth; caudal fin in IP emarginate, this becomes strongly developed in TP.

Colour pattern. Juvenile: schooling groups in life pale grey with series of white flecks on dorsum and sides of body; in Great Barrier Reef waters, juveniles with sprinkling of black cysts over body and fins; solitary individuals often with series of 4 dark longitudinal stripes, 1st on dorsum of body and head, 2nd on mid-body through eye and snout, 3rd on lower body through pectoral fin base on to cheek, 4th (often indistinct) on abdomen (Plate 6D).

IP: body grey to reddish brown shading to light reddish on thorax; dorsal fin light brown with paler distal margin, diffuse dark spot at base of first interspinous dorsal membrane; anal fin reddish brown becoming paler distally; caudal fin light brownish becoming paler distally with narrow whitish distal margin; pectoral fins pale brown to yellowish, diffuse black spot at upper base; pelvic fins brownish red; iris uniform yellow; dental plates white.

IP phase individuals in feeding schools usually pale grey with series of 6-7 diffuse pale spots on dorsum; distal and anterior margins of dorsal, anal and pelvic

fins brownish; posterior region of caudal fin paler with distinct narrow white distal margin; dark blotch on first dorsal interspinous membrane visible. Non-feeding individuals, especially prior to group spawning, uniform dark charcoal-grey with pale whitish snout; distal and anterior margins of dorsal, anal and pelvic fins strongly reddish; caudal grey with distinct pale distal margin (Plate 8A,B).

Preserved body uniform grey with pale distal margin to caudal, with black spot on anterior dorsal membrane and upper pectoral base visible. In some specimens the pale blotches on dorsum are retained.

TP: scales of body green and salmon pink; green pigmentation predominating on dorsum of body and head; green coalescing into 3 green stripes on abdomen, and in some specimens 4 or 5 longitudinal series of spots on caudal peduncle; often yellowish zone covering central region of body from pectoral base to level of first dorsal rays, not extending to abdominal region; lower part of head and thorax pink, purple region on snout at level of eye; blue band on upper lip extending across snout to lower edge of orbit and short distance beyond; 2 blue bands, one central, the other dorsal, from posterior margin of orbit, extending a short distance across head; lower lip blue; blue bar on chin sometimes joining with blue band from upper lip; posterior margin of opercular membrane opposite pectoral base blue; ventral part of head with longitudinal blue band; iris yellow to orange, upper edge green; dental plates white; dorsal and anal fins light orange with broad blue bases and blue distal margins; dorsal fin with median longitudinal series of diffuse green spots which may be partially or completely joined to form a diffuse stripe; dark spot on first spinous dorsal membrane present but indistinct; caudal fin light orange, with blue upper and lower margins and reverse 'D'-shaped blue mark centroposteriorly on fin, vertical part on posterior border of fin, and curved anterior part sometimes broken into spots; pectorals pinkish orange, base and upper rays dark blue, lower rays light blue, lower basal region of fin pink; pelvic fins blue, 2nd and 3rd rays orange.

TP colouration varies in life. Body may be dominated by yellow pigmentation on medial region (Plate 8D) or appear largely green with pinkish ventral regions (Plate 8C). Pink pigment on cheek is characteristic of most TP individuals. Prior to and during spawning, TP individuals become pale pinkish green with distinctive purple blotch on snout at level of eye (Plate 8D). Broad blackish zone on side of body observed in Red Sea spawning individuals (Randall & Ormond, 1978) not obvious in Great Barrier Reef individuals. On preservation, pattern of blue, green and pink markings on snout, head and fins remains distinct.

Remarks. Details of the distribution and reproductive biology of this widespread species are provided in Choat & Robertson (1975), Randall & Ormond (1978), Bruce (1980), and Randall & Bruce (1983). On the Great Barrier Reef it is encountered in moderate numbers on mid-, outer-shelf and Coral Sea reefs. A small scarid

with TP males not usually exceeding 260 mm SL. Great Barrier Reef populations of this species are diandric (Choat & Robertson, 1975), although most spawning appears to occur in pairs or small groups. *Scarus psittacus* is found in a variety of habitats: large groups of small, IP individuals occur in shallow areas beyond reef crests. Small IP individuals are frequently confused with IP *S. globiceps* and small IP *S. rivulatus*. Key features for separating these stages are considered under the species description of *S. rivulatus* (Fig. 5).

The taxonomic status of this species and the identity of the type of *S. psittacus* was clarified by Randall & Ormond (1978). Many previous works and most Australian studies have referred this widespread species to *Scarus forsteri*, a junior synonym. *Scarus psittacus* is present throughout tropical Australia including the west coast, and has often been misidentified in museum collections as *Scarus toshi* and *Xanothon bataviensis*. The type of *Pseudoscarus labiosus* (type locality, Port Moresby) was examined in the Australian Museum and identified as a TP *Scarus psittacus*.

Scarus pyrrhurus (Jordan & Seale)

Plate 3G,H

Callyodon pyrrhurus Jordan & Seale, 1906: 314, fig.55 (type locality, Pago Pago, Samoa).

Callyodon abacurus Jordan & Seale, 1906: 324, pl.23 (type locality, Pago Pago, Samoa).

Scarus capistratoides (not Bleeker).—Schultz, 1969: 22, pl.4E (in part).

Scarus japanensis (not Bloch).—Randall & Choat, 1980: 406, figs 25,26.

Material examined. One specimen, MacGillivray Reef, AMS I.23483-001.

Diagnosis. Median predorsal scales 4; 2 rows of scales on cheek with 5-6 scales in each row; 15 pectoral rays; dental plates exposed; initial phase with 0-2 canines on upper dental plate, terminal phase with 2 canines on upper dental plate; no canines on lower dental plate; canines stout, projecting downward and backward.

Colour pattern. IP: body and head uniform dark brown, slightly paler on cheek; caudal peduncle yellowish; caudal fin orange-red with a narrow black posterior margin; dorsal fin may show faint orange basal band; anal, pectoral and pelvic fins uniform dark brown; dental plates white.

TP: body dark anteriorly and dorsally, greenish yellow posteriorly; caudal peduncle blue-green; dark oblique transverse bar from below anterior dorsal fin to vent, becoming indistinct ventrally; in some specimens, this bar restricted to dorsal region of body; body scales with orange markings, these markings reduced to anterior rim of scales in dark anterior regions of body, as elongate vertical bars in mid-body and ventral regions, and as orange dots on scales of caudal peduncle; top of head and snout purplish grey; cheek orange-yellow; chin and upper lip salmon pink; transverse blue band on chin and upper lip, merging to

form a blue-green band running to and beyond lower margin of orbit; a horizontal green band from upper snout through and beyond upper edge of orbit; short green band passing posteriorly from centre of orbit; dorsal and anal fins blue with median band of orange (broader on dorsal fin), caudal fin blue with dull pink streak in each lobe and pinkish spots in central region of fin; pectoral fins purplish with broad zone of orange on upper part, upper edge blue-green; pelvic fins pale orange with blue lateral edge; dental plates pale bluish.

Remarks. To date only a single specimen has been captured from Australian waters, a 180 mm SL TP male at MacGillivray Reef collected by D.R. Robertson, March 1982. Recent surveys by the authors and A.M. Ayling have recorded isolated groups on mid-shelf and outer reefs (Normanby Island, North-West Reef, Day Reef) of the northern Great Barrier Reef. A single individual was also observed off Townsville outer reefs (G. Russ, pers. comm.), and D. Bellwood observed two IP specimens at Lizard Island.

TP individuals of *S. pyrrhurus* have been identified in the recent literature both as *S. capistratoides* and *S. japanensis*. Recent field work by the junior author has clarified problems associated with these identities. *Scarus japanensis* (Bloch), with a probable type locality of Java, is a senior synonym of *S. capistratoides* Bleeker. *Scarus japanensis* is a west Indian Ocean species with a range which extends to south-west Indonesia. Most previous records of *S. japanensis* from the Indian Ocean appear as *S. capistratoides*.

Scarus pyrrhurus appears to be restricted to the western Pacific from the Ryukyu Islands through the Philippines, the Solomons, eastern Australia to Samoa. Colour illustrations of both IP and TP individuals can be found in the recent literature. Schultz (1969: pl. 4E) illustrates a TP individual from the Philippines identified as *S. capistratoides*. On this specimen the oblique dark zone of the body is reduced. Masuda et al. (1984) and Randall & Choat (1980) have provided colour plates of *S. pyrrhurus* which were misidentified as *S. japanensis*.

As the ranges of *S. japanensis* and *S. pyrrhurus* do not overlap there is no problem of confusion in the field. However, *S. pyrrhurus* may be confused with *S. sordidus* and possibly small *S. bleekeri* in Australian waters. The best field characteristic for IP *S. pyrrhurus* is the orange-red caudal fin. In TP individuals the contrasting dark oblique band, the yellowish green of the posterior body and the blue-green caudal peduncle are characteristic.

Scarus rivulatus Valenciennes

Plates 4C,D; 11D-J

Scarus rivulatus Valenciennes in Cuvier & Valenciennes, 1840: 223 (type locality, Java).

Scarus fasciatus Valenciennes in Cuvier & Valenciennes, 1840: 222 (type locality, Moluccas).

Scarus arcuatus Valenciennes in Cuvier & Valenciennes, 1840: 276 (type locality, Siam).

Pseudoscarus flavolineatus Alleyne & Macleay, 1877: 346, (type locality, Cape Grenville, Queensland, three syntypes AMS I.16373-001)

Material examined. Three SYNTYPES of *Pseudoscarus flavolineatus* AMS I. 16373-001. Two specimens, Heron Island, QM I. 11379, I.11965; one specimen, One Tree Island, AMS I.20498-009; three specimens, Capricorn Reef Group, AMS I.15681-073, I.15683-043; one specimen, Swain Reefs, AMS IB.6085; one specimen, Palm Island, QM I.6416; three specimens, Curacao Reef, QM I.5845, I.6415, I.11390; two specimens, York Island, QM I.6321, I.6322; one specimen, Lizard Island, AMS I.19461-004; two specimens (juveniles), Lizard Island, I.25785-001, I.25796-001; one specimen, Torres Strait, QM I.14992; one specimen, Pt. Quobba, Western Australia, WAM P.12865; one specimen, Kendrew Island, Western Australia, WAM P.22871; one specimen, Rottneet Island, Western Australia, WAM P.25742-006; 82 specimens, Heron Island, not retained; nine specimens, Lizard Island, not retained; one specimen, Moreton Bay, lost after identification and preservation.

Diagnosis. Median predorsal scales 6, rarely 5 or 7, subequal, 3rd or 4th largest, 2 small scales anterior to 1st median predorsal; scale rows on cheek 3, upper and middle rows with 5-7 scales, lower row with 1-3 scales; pectoral rays 14; caudal fin slightly rounded to truncate in juvenile and IP specimens, lobe tips slightly produced in TP; dental plates white, covered by lips; IP without canines; TP usually with 2 small upper and 0-1 lower canines, dorsal profile of snout steep giving characteristic rounded head, especially in terminal phase. Diagnosis of *S. rivulatus* in Randall & Choat (1980) contains a typographical error. Pectoral fins have 14 not 15 rays.

Colour pattern. IP: initial phase has many subtle variants reflecting different aspects of schooling and sexual activity.

(a) In large (especially multispecific) feeding schools: body uniform pale grey to light brown with 2 pale stripes on lower abdominal region; upper margin of eye light blue; dorsal and anal fins light grey to brown, distal margins blue-grey; pectoral fins light grey to brown with upper rays slightly darker, no dark markings at base; caudal and pelvics uniform light grey or brown (Plate 11D).

(b) Single individuals and small feeding schools: body pale yellowish grey; darker mid-body region extending from posterior margin of eye to upper base of caudal fin; scales of central region darker with dusky vertical bars on bases; anterior (behind eye) and posterior (upper caudal peduncle) regions of this darker band distinctly yellow; body and cheek below this central darker region abruptly paler (especially cheek); dorsum of body slightly paler than dark central region (Plate 11F); in smaller individuals yellow colour predominates. Yellowish body colour more pronounced in northern and inshore populations. Interactions amongst feeding IP individuals may be associated with abrupt darkening of central body region giving distinct dark central and abruptly pale ventral region. These individuals have strong resemblance to IP *S. chameleon* (Plate 11G).

(c) Reproductively active individuals: prior to

reproductive activity IP individuals frequently become uniform dark grey with distinct pale abdominal stripes and distinct pale margin to spinous portion of dorsal fin. Group spawning females: body uniform gunmetal grey with distinct dark bars at bases of body scales; uniform darker area on upper head and dorsum extending back to level of 5th dorsal spine; cheek abruptly paler with yellowish tinge (Plate 11H). Group spawning IP males with similar colour pattern but dark bar extending backward from eye, this containing series of dark spots; anterior margin of dorsal fin pale (Plate 11I). In both sexes, pale patch on cheek corresponds to orange cheek patch of TP. Individual females in spawning aggregations may display an overall yellowish colour.

TP: body scales green with basal orange bar, these best developed centrally and posteriorly corresponding to dark scale bars in IP; lower half of operculum bright orange; snout and chin orange with bright green reticulations; regions of dorsal and anal fins blue-green basally, orange centrally with blue margins; dorsal with large green spot in middle of each interradial membrane; caudal fin orange with broad blue dorsal and ventral margins; posterior margin with blue streaks, remainder of caudal membrane with green spots and streaks; pectoral fins chartreuse, upper margin blue-green with submarginal rose streak; pelvic fins orange with broad blue lateral margin.

Reproductively active individuals: body distinctly bicoloured with posterior region (behind level of spinous dorsal) light green, anterior region dark brownish green; pale green strip along anterior dorsum of body below spinous portion of fin; cheek bright orange; pectoral fin standing out sharply against dark anterior background (Plate 11J).

IP individuals become brownish on death and retain this colour on preservation; pale abdominal streaks generally visible. TP individuals gradually lose colour, but relationships between green and orange and blue markings (especially green reticulations on cheek) are detectable after long periods of preservation.

Remarks. Schultz (1969) listed *Pseudoscarus flavolineatus* Alleyne & Macleay as unidentifiable. The three syntypes of *P. flavolineatus* (AMS I.16373-001) proved to be TP specimens of *S. rivulatus* ranging from 235 to 257 mm SL. These all bore clear evidence of the characteristic reticulations around the snout and chin. The original description of Alleyne & Macleay notes only two series of scales on the cheek but all three specimens have the usual three series, each with 2 scales in the ventral row. A more general statement on the taxonomy of *S. rivulatus* is provided by Randall & Choat (1980). Australian collections and literature provide some information on this species. The IP has usually been misidentified and occurs in collections as *Scarus aeruginosus* or *S. dubius*. Examples of the scarid identified as *S. dubius* by Woodland & Slack-Smith (1963) were examined in the University of Queensland Zoology Department (now in the Queensland Museum). These all proved to be IP *S. rivulatus*. Coleman (1981:

pl.237) and Grant (1982: pl.293) provide colour illustrations of the TP. The illustrations of Marshall (1965: 322, pl.48) depicting male and female colour phases are both poor representations of TP individuals and thus males.

Details of the sexual ontogeny of this species and the relationship of sex, size and colour phase are provided by Choat & Robertson (1975). The species is strongly diandric. Subsequent observations of spawning groups of *S. rivulatus* have provided details of the colour phases characteristic of the different sexual identities while spawning (see above). A surprising feature of spawning episodes was the participation of TP individuals in small group spawning episodes involving females and primary males.

Scarus rivulatus is widespread in tropical and subtropical Australian waters and extends beyond the latitude of primary reef environments both on the western (Rottneest Island) and eastern (Moreton Bay) coasts. It is also found on inshore tropical reefs and mangrove areas. This is reflected in the longitudinal distribution pattern in Great Barrier Reef waters. Data provided by D. Williams (pers. comm.) shows that on a cross-shelf transect at 19° S on the Great Barrier Reef *S. rivulatus* was the most abundant scarid on inshore reefs, was also an abundant member of the mid-shelf fauna but was absent from outer-shelf and Coral Sea reefs. These data were collected on windward outer-reef slopes. A.M. Ayling made a similar series of observations (not including Coral Sea reefs) on back reefs and lagoonal areas and encountered *S. rivulatus* in small numbers on outer-shelf reefs. On mid-shelf reefs *S. rivulatus* consistently forms large feeding schools.

Small IP *S. rivulatus* are abundant on mid-shelf reefs and frequently form schools in association with IP of other species, often *S. globiceps* and *S. psittacus*. When viewed underwater the initial phases of these species are difficult to distinguish. Although each species has distinctive elements in their colouration they tend to display very similar patterns when in mixed schools. All can display a uniform light grey colouration with two or three pale abdominal bars. They may however, be distinguished by the following features. *Scarus rivulatus* usually has a lighter colouration than *S. globiceps* with a yellowish caste on the medial regions of the body. The caudal margin is rounded compared with the truncate fins of the other two species. *Scarus globiceps* often displays a temporary series of pale saddles along the dorsum, a feature shared with *S. psittacus*. *Scarus psittacus*, however, has a more acute snout, a distinctive pale posterior margin to the caudal fin and a dark blotch on the anterior dorsal fin. The body is generally a lighter grey than *S. globiceps* and lacks the yellowish caste of *S. rivulatus*. These features are illustrated in Fig.5. When swimming, *S. psittacus* generally holds the caudal fin in a folded position which accentuates the truncate outline of the fin.

Scarus rivulatus is widespread in the western Pacific but does not extend into the Indian Ocean. It is a

moderately large scarid with terminal males reaching 400 mm SL.

Scarus rubroviolaceus Bleeker

Plates 2A,B; 9B,C.

Scarus rubroviolaceus Bleeker, 1847: 162 (type locality, Batavia).

Pseudoscarus rubroviolaceus Bleeker, 1862: 37, pl.13, fig.3. *Pseudoscarus frontalis* Macleay, 1883: 590 (type locality, New Guinea); preoccupied by *Scarus frontalis* Valenciennes in Cuvier & Valenciennes, 1840.

Scarus paluca Jenkins, 1900: 60, fig.18 (type locality, Hawaiian Islands).

Pseudoscarus jordani Jenkins, 1900: 63, fig.20 (type locality, Hawaiian Islands).

Scarus calus Fowler, 1904: 542, pl.21 lower fig. (type locality, Padang).

Callyodon ruberrimus Jordan & Seale, 1906: 316, fig.56 (type locality, Pago Pago).

Callyodon macleayi Jordan & Seale, 1906: 331 (replacement name for *Pseudoscarus frontalis* Macleay).

Pseudoscarus heliotropus Bryan, 1906: 23, fig.3 (type locality, Honolulu).

Pseudoscarus rostratus Gunther, 1909: 315, pl.154 (type locality, Society Islands).

Callyodon africanus Smith, 1955b: 19, pl.3, fig 26, text fig 26 (type locality, Shimon, Kenya).

Material examined. HOLOTYPE of *Pseudoscarus frontalis*, AMS I.16374-001. Two specimens, Heron Island, AMS I.15487-001, I.15498-001; six specimens (juveniles), Lizard Island, AMS I.25790-001, I.25902-001, I.25909-003; one specimen, Heron Island, not retained.

Diagnosis. Median predorsal scales 6; 3 rows of scales on cheek, upper and middle rows with 5–7 scales each, lower row with 1–3 scales; pectoral rays 14–15; lips covering $\frac{1}{3}$ – $\frac{2}{3}$ dental plate, IP with 0–1 canines on upper dental plate, TP with 1–3; snout of adults with characteristic shape, dorsal profile rising sharply from level of eye then curving sharply to straight dorsal profile; each upper pharyngeal bone with 12–14 ridged molariform teeth, no lateral row of small teeth alternating with molars in adults (rudimentary lateral row may be present in juveniles); caudal fin truncate in small IP fish, becoming strongly lunate in large individuals.

Colour pattern. Juvenile (80–130 mm): body light grey, scales with dark posterior margins, body with 3 longitudinal stripes, 1st from occiput along dorsal region to end of dorsal fin, 2nd from tip of snout through eye to centre of caudal peduncle, 3rd across cheek through pectoral base to end of anal fin; body bicoloured with anterior third darker than posterior regions; series of white dots on posterior region of body, these in 4 pairs from body mid-point extending equally spaced to caudal peduncle, dots tending to lie on dark longitudinal lines; median fins greyish, pectorals hyaline. This phase may change rapidly with the dark longitudinal stripes and pale dots being lost or intensified.

IP: body reddish or greyish dorsally and on side, scales with narrow blackish edges and numerous short

radiating black lines, these reduced on head and caudal scales; ventral part of body lighter; body often bicoloured with head and anterior third of body abruptly darker; median fins light reddish to orange, pectoral fins light red on dorsal third becoming paler ventrally, pelvic fins orange-red; iris yellow, dental plates light reddish to white. Colour in life usually greyish white posteriorly with the anterior third abruptly reddish-brown, this pattern usually fading to uniform reddish on death.

TP: body green dorsally, fading to greenish yellow on sides, scales with light orange vertical bar, body becoming blue-green ventrally, caudal peduncle lighter green; edge of upper lip narrowly salmon pink with broad band of blue-green above it, edge of lower lip blue-green; chin salmon pink, crossed by blue-green bar which joins with blue-green bar on lower lip and continues dorsally as blue line to lower margin of orbit; horizontal blue-green streak through upper margin of eye and single blue-green postorbital bar; longitudinal green line on lower cheek; dorsal fin orange with blue-green distal margin, blue-green marking on each ray, these becoming reduced posteriorly; anal fin orange with broad blue-green distal margin and basal line of blue-green blotches; caudal with upper and lower margins blue, central part light orange this colour extending onto upper and lower caudal rays, posterior portion of fin with thin orange margin; pectorals broadly blue-green on upper edge, usually horizontal light orange streak below this, rest of fin blue-green becoming paler ventrally; pelvic fins orange with broad blue anterior margin; iris orange, dental plates dark green, edged with white.

In life TP individuals on the Great Barrier Reef may also be bicoloured with anterior third of body dark green and posterior $\frac{2}{3}$ light green.

Remarks. This species has a very wide distribution, extending from East Africa to the coast of tropical eastern America. Minor differences in colouration occur in different parts of the range (eg. bicolouration of the IP is not as distinct in Indian Ocean material) but the basic colour pattern described above is maintained over this wide geographic area. This species is common in southern New Guinea where both colour phases were recorded by Munro (1967).

The type of *Pseudoscarus frontalis* (AMS I. 16374-001, 360 mm SL) proved to be an IP *S. rubroviolaceus* and represents the first record of this species from New Guinea. *Pseudoscarus frontalis* Macleay has had a confused history, being initially referred to *S. gibbus* by Schultz (1958) and later to *B. muricatum* by Schultz (1969). As the name *frontalis* was preoccupied, Jordan & Seale proposed the replacement name *macleayi*, under which name it was included by Schultz (1969) in the synonymy of *Bolbometopon muricatum*.

This species is one of a member of a group of large scarids including *C. bicolor* which is characteristic of reef-crest areas; it is usually encountered as solitary

individuals or in pairs. Although never observed to be common on the Great Barrier Reef, it has a wide distribution across the shelf, occurring on the crests and outer slopes of reefs from the mid shelf to the Coral Sea. This species has not been recorded from Western Australia, but three specimens were collected in Arnhem Land, northern Australia (Taylor, 1964). It attains a large size, approximately 500 mm SL in terminal males. A 502 mm SL terminal male was collected at Heron Island.

Scarus schlegeli (Bleeker)

Plates 2G,H; 7D-I

Pseudoscarus Schlegeli Bleeker, 1861: 242 (type locality, Celebes).

Pseudoscarus pentazona Bleeker, 1861: 241 (type locality, Celebes).

Scarus cypho Seale, 1901: 95 (type locality, Guam).

Material examined. One specimen, One Tree Island, AMS I.15647-065; one specimen, Keeper Reef, QM I.6999; eleven specimens, Lizard Island, AMS I.15647-065, I.19445-014, I.19445-016, I.19471-006; one specimen, Abrolhos Islands, WAM P.25307-001; one specimen, Pelsart Island, Western Australia, WAM P.84; one specimen, Northwest Cape, WAM P.12866; four specimens, Enewetak, BPBM 6256, 6301; two specimens, Rapa, BPBM 12835, 13008; one specimen, Okinawa, BPBM 22266; one specimen, Papeete, BPBM 6128; two specimens, Ponape, Carolines, BPBM 9694; 35 specimens, Heron Island, not retained; six specimens, Lizard Island, not retained.

Diagnosis. Median predorsal scales 4, subequal, second scale largest; 2 rows of cheek scales; upper row with 6–7 scales, lower row with 5–7 scales; pectoral rays 14, occasionally 15; caudal fin of initial phase slightly rounded, terminal phase with lobes slightly produced giving double emarginate effect; dental plates nearly covered by teeth; IP fish lacking canines on dental plates; TP males usually with a single canine on upper dental plate and 2 on lower; small TP individuals may lack these completely.

Colour pattern. Juvenile: body dark brown with 5 pale vertical bars, first beneath 5th dorsal spine, last on caudal peduncle; snout and chin paler, each with faint transverse bluish band; median and caudal fins dark brownish; pectoral fins hyaline with slightly darker upper rays and base. In life, general impression is of dark fish with indistinct pale vertical bars (Plate 7D); when juvenile fish are schooling, bars may be absent. Small individuals may be confused with IP *S. spinus* (cf Plate 7C,D).

IP: body colouration ranges from pale brownish to darker purplish brown; in paler individuals faint orange bars at bases of body scales may be detected; 5 pale vertical bars on body as in juvenile phase, these varying in development and intensity, but always visible; snout pale grey to orangish with pale bluish margin to upper and lower lip, bluish bar on chin, faint bluish band extending from corner of mouth to anterior margin of eye; median fins brownish to light orange with medial

series of bluish blotches; distal margins blue; caudal fin light brownish with vertical faint green markings; pectoral fins pale with indistinct dark spot at upper base; pelvic fins with light brownish anterior margins. When feeding in small groups, background colouration in IP individuals may be pale grey (especially on the anterior regions) with expanded pale vertical bars; this gives an impression of a pale mottled fish (compare Plate 7E & F). In larger schools and especially when moving to and at spawning sites, body purplish with narrowed and sometimes indistinct pale vertical bars. Females retain this pattern while spawning. IP males in spawning aggregations distinguished by uniform dark colouration of body and fins with vertical pale bars being reduced to indistinct pale saddles on dorsum. Anterior dorsal region from 3rd dorsal spine to snout tip paler, this pale area not extending below lower margin of eye (corresponds to lilac dorsal patch developed in spawning TP individuals); distal margin of spinous portion of dorsal fin pale; dental plates white.

TP: body dark greenish, margins of scales broadly edged with orange-red, this colour best developed on scale bases; anterior dorsal region of body back to 6th dorsal spine solid green to greenish grey, this colour not extending below lower margin of orbit; body with greenish yellow band extending from dorsal spines VII–IX to origin of anal fin; this band covers 10th to 13th scale rows of dorsum; upper region of this band bright yellow; anterior regions of body and head below dorsal green area dark brown to greenish, cheek slightly paler; snout pale reddish to brown; lips edged with blue; distinct pale bar on chin (in some specimens this may extend as faint line to eye); chin and isthmus paler; broad blue-green band from corner of mouth to anterior margin of eye; 2 horizontal green bands extending backward from eye; subopercle blue-green; dark green medial stripe extending from isthmus to vent; median fins orange, spotted with green, spots in single median row on dorsal and anal fins, usually confluent to form single median line on anterior dorsal and anal fins, distal margins of fins blue-green; caudal fin with spots aligned in 3 vertical bands; dorsal and ventral margins of caudal fin blue-green; pectoral fins pale greenish, becoming light brownish dorsally, base and upper margin blue-green, a dark spot in upper corner of pectoral base; pelvic fins blue with band of orange on first soft ray; dental plates greenish. During spawning episodes the following modifications occur in terminal colour pattern: body becomes dark brown to purplish overall; anterior dorsal green region becomes intense lilac colour with pinkish blotch over anterior region of snout; dorsal yellow spot and transverse greenish bar strongly emphasised against general darkening of body.

Major characteristic of living TP specimens is green area on head and dorsum, yellow dorsal patch and transverse band. These contrast strongly with dark body colouration. On removal from water these contrasts immediately reduced. In IP individuals removal from water is often followed by lightening of body colouration and loss of definition of pale bars.

On preservation most body markings of terminal phase are lost although blue-green markings on head and fins, and position of transverse bar and its yellow pigment remain distinct. IP individuals uniform dark brown after preservation with bluish bars on snout and chin remaining distinct. Preserved IP specimens are often confused with *S. psittacus*.

Colour transitional individuals of *S. schlegeli* (Plate 7G) are observed more frequently than in most other species of scarids.

Remarks. This species has previously been misidentified as *Scarus venosus*. However *S. venosus* is a junior synonym of *S. psittacus*, and *S. schlegeli* was therefore re-established as the valid name for this species (Randall & Choat, 1980). *Scarus schlegeli* is present in the western and central Pacific and the Indonesian Archipelago. It is replaced in the western Indian Ocean by the closely related *Scarus russelli* Valenciennes (Randall & Bruce, 1983). The Red Sea representative of this complex is *S. fuscopurpureus* (Fig.2).

TP specimens of *S. schlegeli* from the Great Barrier Reef differ from those in the central and western Pacific (Compare Plate 7 H & I). The main differences are in the disposition and extent of the transverse bar and associated vertical markings but there are also minor differences in fin shape and body proportions. Specimens from the Indo-west Pacific and northern tropical regions have two pale transverse bars on the body; the first below the 8th and 9th dorsal spines, and the second below the 3rd and 4th dorsal rays, commencing at the 14th scale row on the dorsum; these bars are separated by a dark area on the dorsum at the 12th and 13th scale rows; the anterior bar does not usually extend to the abdominal region and may be lost on death; the second bar extends the entire width of the body; both bars have characteristic bright yellow marks on the dorsal region; the body between the two transverse bars and immediately posterior to the second bar may be slightly darker. The greatest body depth is contained three times in the standard length.

TP individuals from the Great Barrier Reef and the southern Pacific (four specimens from Rapa and Tahiti examined in the Bishop Museum) display only a single transverse bar with the yellow marking below the 7th to 9th dorsal spines as described above. The greatest body depth is contained 2.4–2.6 times in the standard length. Five specimens from Okinawa, the Marshalls and the Carolines show the double transverse bars. The Great Barrier Reef material seems to be part of a southern Pacific distribution of this colour variant. The status of these variants is unclear. Bleeker's figure (1862: pl.12 fig.2) of a TP specimen from the Celebes (now Sulawesi) shows clearly that the original description refers to the central Pacific colour variant as does the original description of *Scarus cypho*. A specimen from the Abrolhos Islands, Western Australia (W.A. Museum P25307-001) display the double transverse bar colour pattern. More collecting in northern Australian waters is required to clarify the status of the TP colour variants. A number of recent works have provided good

illustrations of the central Pacific form of TP *S. schlegeli*. Schultz (1969: pl. 4A) shows a TP individual from the Philippines; Masuda et al. (1984) show a specimen from Japanese waters clearly illustrating the disposition of the transverse bars. Randall & Choat (1980: fig. 20) show the characteristic position of the yellow marking in central Pacific specimens.

Scarus schlegeli is a common scarid of sheltered habitats on mid-shelf reefs. Members of small feeding schools may often be observed browsing the algal and diatom covering of sand flats in lagoonal or deep reef habitats. It frequently forms mixed feeding schools with other scarids. This species is weakly diandric (Choat & Robertson, 1975). Both group and pair spawning have been observed at Lizard Island. Group spawning involved only 4 to 5 initial phase males. It is a scarid of moderate size, with terminal males reaching approximately 300 mm SL.

Scarus sordidus Forsskål
Plates 3I,J; 6E; 8E,F,G,H

- Scarus sordidus* Forsskål, 1775: X, 30 (type locality, Red Sea).
Scarus erythron Valenciennes in Cuvier & Valenciennes, 1840: 255 (type locality, Mauritius).
Scarus variegatus Valenciennes in Cuvier & Valenciennes, 1840: 256 (type locality, Mauritius).
Scarus purpureus Valenciennes in Cuvier & Valenciennes, 1840: 277 (type locality, Ulea = Woleai, Caroline Islands; preoccupied by *Scarus purpureus* Forsskål, 1775).
Scarus spilurus Valenciennes in Cuvier & Valenciennes, 1840: 279 (type locality, Caroline Islands).
Scarus gymnognathos Bleeker, 1853a: 498 (type locality, Batavia).
Scarus celebicus Bleeker, 1854c: 253 (type locality, Makassar, Celebes).
Pseudoscarus Goldiei Macleay, 1883: 590 (type locality, New Guinea).
Pseudoscarus margaritus Cartier, 1874: 105 (type locality, Cebu, Philippines).
Callyodon cyanogrammus Jordan & Seale, 1906: 330, fig. 63 (type locality, Apia, Samoa).
Pseudoscarus vitriolinus Bryan, 1906: 27, fig. 4 (type locality, Honolulu).
Callyodon rostratus Seale, 1909: 524, (type locality, Zamboanga, Mindanao; homonym of *Scarus rostratus* Poey).
Callyodon albipunctatus Seale, 1909: 526 (type locality, Sitanki Island, Jolo Archipelago, Philippine Islands).
Callyodon bipallidus Smith, 1955a: 936 (type locality, Pinda, Mozambique).

Material examined. HOLOTYPE of *Pseudoscarus goldei*, AMS I.16376-001. One specimen, Lord Howe Island, AMS I.17367-012; one specimen, Heron Island, AMS IB. 3862; seven specimens, One Tree Island, AMS I.15632-011, I.20205-023, I.20213-004, I.20826-016; one specimen, Sir Charles Hardy Island, I.20770-062; one specimen, Broadhurst Reef, QM 10353; three specimens, Escape Reef, AMS I.22601-008, I.22611-009, I.22586-041; 15 specimens, Lizard Island, AMS I.18739-020, I.18755-102, I.19444-008, I.19462-001, I.19482-105; one specimen, Rowley Shoals, Western Australia, WAM P.27658-035; 30 specimens, Heron Island, not retained; 18 specimens, Lizard Island, not retained.

Diagnosis. Median predorsal scales 4, subequal becoming progressively larger anteriorly; 2 rows of cheek scales, upper with 5–7 scales, lower with 5–7 scales; pectoral rays 14–15, usually 15; mouth terminal, dental plates broadly exposed, lips covering less than half plates; large individuals with up to 2 canines on side of upper dental plate, none on lower.

Colour pattern. Juvenile: body white to pale brownish with 4 dark brown to black longitudinal stripes, first from occipital region along dorsum to end of dorsal fin, 2nd from snout through eye to caudal peduncle, 3rd from chin through pectoral base to caudal peduncle, 4th from opercular margin along abdomen to end of anal fin; dark mid-dorsal stripe along base of dorsal fin, ends of 2nd and 3rd longitudinal stripes may be enlarged to form black blotch at base of caudal peduncle; fins pale hyaline brown, lacking any distinctive markings. Intensity of dark stripes may vary rapidly in same individual to extent that black stripes merge into a darker background colouration.

IP: body dark brown scales sometimes edged in dull yellow, general body colouration becoming paler anterodorsally, 2 longitudinal rows of 3–4 whitish spots often present on the darker posterior region of body; head grey-brown shading to light red ventrally and around mouth, dental plates pale salmon becoming whitish on edges, series of yellowish reticulations on head across interorbital and especially on post-orbital region, cheek scales faintly edged in yellowish brown, iris yellow; dorsal fin reddish brown; anal, caudal and pelvic fins brown; pectoral fins with pale membranes and dark brown rays. Body of IP and large juvenile individuals may be darker brown overall with caudal peduncle and fin abruptly greyish white with large round dark spot in centre of the caudal peduncle. These colour patterns may interchange rapidly in the same individual.

TP: body green with edges of scales pinkish; caudal peduncle and base of fin light green; thorax and abdomen bluish, often with a pink caste, with 2 longitudinal green stripes and median green ventral stripe from chin to vent; occiput green with snout bluish green; sides of head above cheek faintly pink, cheek green then yellowish to orange ventrally; 2 green postorbital bands, upper extending anterior to orbit, green band on snout and broad green band on chin joining behind mouth to form diffuse green line running to posterior margin of orbit and opercular margin; dental plates green; basal region of dorsal fin green, medial region pinkish with dark green spots on each interradiation membrane, outer margin dark green; anal fin with narrow basal green area, pink stripe then broad green band; caudal fin dark green or bluish green, upper and lower margins green with submarginal pink zone (fin membranes may be pinkish); pectorals pale green with upper and medial rays darker green; pelvics pale green, spine and anterior rays darker green.

Small TP individuals often darker green overall with abruptly paler caudal peduncle (Plate 8G); larger individuals paler. When reproductively active, dorsoposterior region of body becomes yellow (Plate

8H), remainder of body yellowish green with snout and caudal fin bluish.

Remarks. Randall & Bruce (1983) provided a review of some aspects of the synonymy of *S. sordidus* which belongs to a complex of closely related species, most of which replace each other in a series from the Red Sea to the central Pacific. Apart from *S. sordidus*, which occurs across the whole range of this complex, Great Barrier Reef waters harbour the closely related *S. pyrrhurus* which is the western-most member of this series. This species was recorded from New Guinea by Munro (1967) as *Xanothus erythrodon* and *S. sordidus*.

Scarus sordidus is one of the most abundant and widely distributed of all scarids. It is probably the commonest scarid on the Great Barrier Reef and one of the few to occupy all the reef habitats examined. *Scarus sordidus* is consistently abundant through mid-shelf, outer and Coral Sea reefs (D. Williams, pers. comm.). It extends through northern Australian waters into Western Australia where it may be found in temperate reef environments (Hutchins & Thompson, 1983). This species is diandric; its reproductive behaviour appears to be highly variable, with populations in deeper water having a smaller proportion of primary males than those on the reef crest (Choat & Robertson, 1975). Group spawning has not been observed on the Great Barrier Reef although it is highly probable that it occurs in a fashion similar to that seen in *S. schlegeli*.

Scarus spinus (Kner)

Plates 3A,B; 7C

Pseudoscarus spinus Kner, 1868: 354, pl. 9, fig. 27 (type locality, Kandavu, Fiji Islands).

Callyodon kelloggi Jordan & Seale, 1906: 327, fig. 62 (type locality, Apia, Samoa).

Material examined. Two specimens, One Tree Island, AMS I.20582-003, I.20583; one specimen, Escape Reef, AMS 22611-009; three specimens, Lizard Island, AMS I.19445-015, I.19462-012, I.19473-034; ten specimens, Heron Island, not retained.

Diagnosis. Median predorsal scales generally 4, but varies from 3–5 (anterior scale may be small and embedded); directly anterior to first median scale (hence above posterior part of eye) a transverse pair of smaller scales which overlap medially in mid-dorsal line, these not counted as median predorsals; rows of scales on cheek 3, upper row 5–7 scales (usually 5) middle row with 5–7 scales, ventral row with 1–2 (usually 2) scales; pectoral rays 13–14 (usually 14); caudal fin of IP slightly rounded to truncate, of TP moderately to deeply emarginate; dental plates covered by lips; adults in IP generally with no canines on upper dental plate and 1 on lower; TP fish with 1–2 upper canines and 1–2 lowers, the lowermost (when there are 2) very large and projecting diagonally backward. Shape of front of head of TP distinctive, being bluntly rounded, dorsal and

ventral profiles being almost identical. Heads of IP fish not as obtuse.

Colour pattern. IP: body dark brown with distinctive velvety appearance, shading on side of head and ventrally on head and body to reddish brown; body with 4–5 indistinct pale bars 1–2 scales in width (bars formed by pale central parts of scales), 1st beneath 3rd to 4th dorsal spines, 2nd below 8th dorsal spine, 3rd below 3rd–4th dorsal rays, 4th below 8th–9th dorsal rays, and 5th, when visible, crossing caudal peduncle; fins reddish brown except membranes of about lower $\frac{2}{3}$ of pectoral fins which are pale; dental plates white. In life, pale bars may appear almost white; fish can turn this pattern on and off rapidly. Care should be taken when identifying IP individuals underwater to ensure that they are not confused with small IP *S. schlegeli*. (See Plate 7 C&D).

TP: Scales of body green, narrowly edged in rose; most of upper lip and snout above it chartreuse; operculum and cheek yellow to yellowish; broad zone of blue-green from interorbital down side of snout to lower lip and chin; nape green; large individuals may have pale rose to violet streak passing ventrally from front of eye; upper lip narrowly salmon (though this colour may not be continuous along entire margin); 2 large curved transverse salmon bands on chin, uppermost nearly reaching margin of lower lip and ending just below corner of mouth; dorsal and anal fins with basal band of green, median band of salmon, and margin of blue; unscaled part of caudal fin with blue lobes, each containing median streak of salmon to orange, broad hemispherical posterior part of fin green; upper half of pectorals blue-green with streak of rose, lower half greenish shading to pale distally; pelvic fins blue to blue-green with broad band of orange submarginal to lateral edge. Coleman (1981) provides an excellent underwater illustration of a TP individual.

Remarks. This parrotfish has been previously identified in the literature as *Scarus formosus* Valenciennes. A review of recent taxonomic changes and the distribution of this species is provided by Randall & Choat (1980). *Scarus spinus* is known from the Philippines and the western and central Pacific; it is very similar to *Scarus viridifucatus* of the Indian Ocean. On the Great Barrier Reef it is most common on mid-shelf reefs but has also been observed on outer shelf and Coral Sea reefs. It is characteristic of reef crest and the shallower parts of outer-reef slope habitats. *Scarus spinus* feeds individually or may join mixed schools. It is nowhere abundant. Pair spawning has been observed and the species is diandric. It is one of the smaller scarids on the Great Barrier Reef, the largest individual collected being 225 mm SL.

ACKNOWLEDGEMENTS. The Great Barrier Reef Marine Parks Authority provided funding for the preparation and publication of the colour plates. We wish to thank Wendy Craik and Alister Gilmore for their assistance in securing and administering these funds. Access to Reef study sites was provided by an MST grant administered by the Australian Museum. The following Institutions provided assistance: the Australian Museum, the Bishop Museum, the Australian Institute of Marine Sciences, the University of Sydney, the University of Queensland, James Cook University and the University of Auckland. Field assistance was provided by the Lizard Island, One Tree Island and Heron Island Research Stations. We wish to thank J. Paxton, B. Goldman, D. Williams and P. Sale for assistance in this respect.

This study was assisted greatly by the contributions of A. Ayling, D. Williams, G. Russ, D. Bellwood and P. Doherty who provided information on scarid distribution patterns from various parts of the Great Barrier Reef and the Coral Sea. R. Robertson provided us with crucial information, colour photos and specimens of scarids. R. Kuiter also provided us with important colour photos of scarids. J. Lavas provided colour drawings and diagrams.

Assistance with taxonomic studies, museum material and references was provided by J. Paxton and J. Leis (Australian Museum), R. McKay (Queensland Museum) and G. Allen (Western Australian Museum). B. Russell and M. Gomon also provided assistance with records and location of types.

Introductory aspects of Great Barrier Reef scarid investigations were greatly helped by J.M. Thomson and F.H. Talbot.

This project benefited from discussions with B. Goldman, J. Leis, R. Thresher, P. Sale, G. Jones, V. Springer, and especially J. Paxton. Drafts of the manuscript were improved by the criticism and comments of B. Russell, J. Paxton, J. Leis and D. Bellwood.

References

- Allen, G.R., D.F. Hoese, J.R. Paxton, J.E. Randall, B.C. Russell, W.A. Starck II, F.H. Talbot & G.P. Whitley, 1976. Annotated checklist of the fishes of Lord Howe Island. Records of the Australian Museum 30: 365–454.
- Alleyne, H.G. & W. MacLeay, 1877. The ichthyology of the Chevert Expedition. Proceedings of the Linnean Society of New South Wales 1: 321–359.
- Baker, J.T., R.M. Carter, P.W. Sammarco & K.P. Stark, 1983. Proceedings of the Inaugural Great Barrier Reef Conference. JCU Press, Townsville, 545 pp.
- Beaufort, L.F.De., 1940. The fishes of the Indo-Australian Archipelago 8: 1–508.
- Bennett, J.W., 1834. A selection of rare and curious fishes found upon the coast of Ceylon. 2nd ed., London, 30 pp.
- Blaber, S.J.M., J.W. Young & M.C. Dunning, 1985. Community structure and zoogeographic affinities of the coastal fishes of the Dampier region of North-western Australia. Australian Journal of Marine and Freshwater Research 36: 247–266.
- Bleeker, P., 1847. Pharyngognathorum Siluroideorumque species novae javanenes. Natuur- en Geneeskundig Archief voor Neds Indie (2) 4: 155–169.
- , 1853a. Diagnostische beschrijvingen van nieuwe of weinig bekende vischsoorten van Batavia. Natuurkundig Tijdschrift voor Nederlandsch-Indië 4: 451–516.

- 1853b. Nieuw bijdrage tot de kennis der ichthyologische fauna van Ternate en Halmaheira (Gilolo). *Natuurkundig Tijdschrift voor Nederlandsch-Indië* 4: 595–610.
- 1854a. Bijdrage tot de kennis der ichthyologische fauna van Halmaheira (Gilolo). *Natuurkundig Tijdschrift voor Nederlandsch-Indië* 6: 49–62.
- 1854b. Species piscium bataviensium novae vel minus cognitae. *Natuurkundig Tijdschrift voor Nederlandsch-Indië* 6: 191–202.
- 1854c. Vijfde bijdrage tot de kennis der ichthyologische fauna van Celebes. *Natuurkundig Tijdschrift voor Nederlandsch-Indië* 7: 225–260.
- 1854d. Specierum piscium javanensium novarum vel minus cognitatum diagnoses adumbratae. *Natuurkundig Tijdschrift voor Nederlandsch-Indië* 7: 415–488.
- 1855a. Visschen van de Duizendeilanden. *Natuurkundig Tijdschrift voor Nederlandsch-Indië* 8: 344.
- 1855b. Zesde bijdrage tot de kennis der ichthyologische fauna van Amboina. *Natuurkundig Tijdschrift voor Nederlandsch-Indië* 8: 391–434.
- 1859. Bijdrage tot de kennis der vischfauna van Nieuw-Guinea. *Naturkundige Vereeniging in Nederlandsch-Indië, Batavia, Verhandelingen* 6: 1–21.
- 1861. Iets over de geslachten den Scaroiden en hunne Indisch-archipelagische soorten. *Verslagen en Mededeelingender Koninklijke Akademie van Wetenschappen, Amsterdam* 12: 228–244.
- 1862. *Atlas Ichthyologique des Indes Orientales Néerlandaises, publië sous les auspices du gouvernement colonial Néerlandais* I. Frédéric Muller, Amsterdam, 168 pp.
- Bloch, M.E. & J.G. Schneider, 1801. *Systema Ichthyologiae Iconibus CX Illustratum*. Sanderiano Commissum, Berolini, 584 pp.
- Bruce, R.W., 1980. On the occurrence of very small terminal phase parrotfishes. *Copeia* 4: 887–889.
- Bruce, R.W. & J.E. Randall, 1985. A revision of the Indo-West Pacific parrotfish genera *Calotomus* and *Leptoscarus* (Scaridae: Sparisomatinae). *Indo-Pacific Fishes*, 5: 1–32.
- Bryan, W.A., 1906. Three new Hawaiian Fishes. *Occasional papers of the Bernice P. Bishop Museum* 2(4): 22–37.
- Cartier, O., 1874. Beschreibungen neuer Pharyngognathen; ein Beitrag zur Kenntniss der Fische des philippinischen Archipels. *Verhandlungen der Physikalisch-medizinischen Gessellschaft zu Würzburg n.s.* 5: 96–105.
- Castelnau, F., 1875. Researches on the fishes of Australia. *Philadelphia Centennial Exhibition of 1876 (Melbourne 1875)* 2: 1–52.
- Choat, J.H. & D.R. Robertson, 1975. Protogynous hermaphroditism in fishes of the Family Scaridae. In "Intersexuality in the Animal Kingdom" (R. Reinboth ed.): 263–283, Springer-Verlag, Heidelberg.
- Choat, J.H. & D.R. Bellwood, 1986. Interactions amongst herbivorous fishes on a coral reef: influence of spatial variation. *Marine Biology* 89: 221–234.
- Coleman, N., 1981. Australian sea fishes north of 30°S. Doubleday, Australia Pty. Ltd., 297 pp.
- Cuvier, G.L. & M.A. Valenciennes, 1840. *Histoire Naturelle des Poissons*. 14: 1–464, Pitois-Levrault, Paris.
- DeVis, C.W., 1885. New fishes in the Queensland Museum. *Proceedings of the Linnean Society of New South Wales* 9: 869–887.
- Forsskal, P., 1775. *Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali*. Mölleri Hauniae, 164 pp.
- Fourmanoir, P. & P. Guézé, 1961. Les poissons de la Réunion. II. Familles des Labridae, Callyodontidae, Malacanthidae. *Publications Institut de Recherches Scientifique Tananarive*: 1–21.
- Fowler, H.W., 1899. Observations of fishes from the Caroline Islands. *Proceedings of the Academy of Natural Sciences of Philadelphia* 51: 482–596.
- 1904. A collection of fishes from Sumatra. *Journal of the Natural Academy of Sciences of Philadelphia*, 2nd Series 12: 467–560.
- Fowler, H.W. & B.A. Bean, 1928. Contributions to the biology of the Philippine Archipelago and adjacent regions. The fishes of the Families Pomacentridae, Labridae, and Callyodontidae. *Bulletin of the United States National Museum* 100 7: 1–502.
- Gilbert, C.H., 1890. A preliminary report on the fishes collected by the steamer *Albatross* on the Pacific Coast of North America during the year 1889, with descriptions of twelve new genera and ninety-two new species. *Proceedings of the United States National Museum* 13: 49–126.
- Gilchrist, J.D.F. & W.W. Thompson, 1909. Descriptions of fishes from the coast of Natal. *Annals of the South African Museum* 6: 213–279.
- Gomon, M.F. & J.R. Paxton, 1985. A revision of the temperate fishes of the labroid family Odacidae. *Indo-Pacific Fishes* 8: 1–57.
- Gosline, W.A. & V.E. Brock, 1960. *Handbook of Hawaiian Fishes*. University of Hawaii Press, Honolulu, 372 pp.
- Grant, E.M., 1982. *Guide to Fishes* (5th ed.) Department of Harbours and Marine, Brisbane, 896 pp.
- Gray, J.E., 1854. Catalogue of fish collected and described by L.T. Gronow, now in the British Museum. Woodfall and Kinder, London, 196 pp.
- Günther, A., 1909. Andrew Garrett's Fische der Südsee. *Journal des Museum Godeffroy* 4: 1–534.
- Heller, E. & R.E. Snodgrass, 1903. Papers from the Hopkins Stanford Galapagos Expedition, 1998–1899, XV: New Fishes. *Proceedings of the Washington Academy of Sciences* 5: 189–229.
- Herre, A.W., 1933. Twelve new Philippine fishes. *Copeia* 1: 17–25.
- Hutchins, B. & M. Thompson, 1983. The marine and estuarine fishes of south-western Australia. *Western Australian Museum*, 103 pp.
- Jenkins, O.P., 1900. Descriptions of new species of fishes from the Hawaiian Islands belonging to the families Labridae and Scaridae. *Bulletin of the United States Fish Commission* 19: 45–65.
- 1903. Report on collections of fishes made in the Hawaiian Islands with descriptions of new species. *Bulletin of the United States Fish Commission* 22: 417–511.
- Jenyns, L., 1842. Fish. In "The Zoology of the Voyage of H.M.S. Beagle", part 4: 1–172.
- Jordan, D.S. & B.W. Evermann, 1903. Descriptions of new genera and species of fishes from the Hawaiian Islands. *Bulletin of the United States Fish Commission* 22: 161–208.
- Jordan, D.S. & A. Seale, 1906. The fishes of Samoa, descriptions of the species found in the archipelago, with a provisional check-list of the fishes of Oceania. *Bulletin of the Bureau of Fisheries* 25: 175–488.
- Kaufman, L.S. & K.F. Liem, 1982. Fishes of the suborder Labroidea (Pisces: Perciformes): phylogeny, ecology, and evolutionary significance. *Breviora* 472: 1–19.
- Kner, R., 1866. Reise der österreichischen Fregatte 'Novara' um die Erde in den Jahren 1857–1859 unter den Befehlen des Commodore B. von Wüllerstorff-Urbain. *Zoologischer*

- Theil, Fische. 1(2): 114-272.
- . 1868. Ueber neue Fische aus dem Museum der Herren Johann Cäsar Godeffroy & Sohn in Hamberg. 4,2. Sitzungsberichte der Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe, Wien 58: 293-356.
- Lacépède, B.G., 1802. Histoire naturelle des poissons 4: 1-728, Plassan, Paris.
- Macleay, W., 1883. Contributions to a knowledge of fishes of New Guinea. No. 3. Proceedings of the Linnean Society of New South Wales (1) 7: 585-598.
- Marshall, T.C., 1964. Fishes of the Great Barrier Reef and coastal waters of Queensland. Angus and Robertson, Sydney, 566 pp.
- Masuda, H., 1984. Field pictorial dictionary of marine fishes. Tokai University Press, Tokyo, 277 pp. In Japanese.
- Masuda, H., K. Amaoka, C. Araga, T. Uyeno & T. Yoshino, (editors) 1984. The fishes of the Japanese Archipelago. Tokai University Press, Tokyo, 437 pp.
- McCulloch, A.R., 1930. A check-list of the fishes recorded from Australia. Australian Museum Memoirs 5(1-4): 1-534.
- Meek, S.E. & S.F. Hildebrand, 1928. The marine fishes of Panama. Publications of the Field Museum of Natural History No. 249. Zoological Series 15(3): 709-1045.
- Munro, I.S.R., 1967. The fishes of New Guinea. Department of Agriculture, Stock and Fisheries, Port Moresby, 651 pp.
- Ogilby, J.D., 1915. Ichthyological Notes (No.2). Memoirs of the Queensland Museum 3: 130-136.
- Paradise, W.E.J. & G.P. Whitley, 1927. Northern Territory Fishes. Memoirs of the Queensland Museum 9(1): 76-106.
- Pellegrin, J., 1901. Poissons recueillis par M. Lion Diquet dans le Golf de Californie. Bulletin du Museum d'Histoire Naturelle, Paris 7: 160-167.
- Playfair, R.L. & A.C.L. Gunther, 1867. The fishes of Zanzibar. John van Voorst, London, 153 pp.
- Quoy, J.R.C. & P. Gaimard, 1824. Voyage autour du monde 'l'Uranie' et 'la Physicienne'. Zoology: 182-401.
- Randall, J.E., 1963. Notes on the systematics of parrotfishes (Scaridae) with emphasis on sexual dichromatism. Copeia 2: 225-237.
- Randall, J.E. & R.W. Bruce, 1983. The parrotfishes of the subfamily Scarinae of the western Indian Ocean with descriptions of three new species. Ichthyological Bulletin Rhodes University 47: 1-39.
- Randall, J.E. & J.H. Choat, 1980. Two new parrotfishes of the genus *Scarus* from the central and south Pacific, with further examples of sexual dichromatism. Zoological Journal of the Linnean Society 70(4): 383-419.
- Randall, J.E. & R.F.G. Ormond, 1978. On the Red Sea parrotfishes of Forsskal, *Scarus psittacus* and *Scarus ferrugineus*. Zoological Journal of the Linnean Society 63: 239-248.
- Richardson, J., 1844-1855. Ichthyology, in Zoology of the voyage of H.M.S. 'Sulphur'. Smith, Elder & Co., London, 150 pp.
- . 1846. Report on the ichthyology of the seas of China and Japan. Report of the British Association for the Advancement of Science 1845: 187-320.
- Robertson, D.R. & R.R. Warner, 1978. Sexual patterns in the labroid fishes of the western Caribbean, II. The Parrotfishes (Scaridae). Smithsonian Contributions to Zoology 255: 1-26.
- Robertson, D.R., R. Reinboth & R.W. Bruce, 1982. Gonochorism, protogynous sex-change and spawning in three Sparisomatine parrotfishes from the western Indian Ocean. Bulletin of Marine Science 32(4): 868-879.
- Rosenblatt, R.H. & E.S. Hobson, 1969. Parrotfishes (Scaridae) of the eastern Pacific, with a generic rearrangement of the Scarinae. Copeia 3: 434-453.
- Rüppell, E., 1828-1830. Atlas zu der Reise im nördlichen Afrika. Fisches des rothen Meeres. Heinr. Ludw. Brönnner, Frankfurt am Main, 141 pp.
- . 1835-1838. Neue Wirbelthiere der Fauna von Abyssinien gehorig. Fische des rothen Meeres, Siegmund Schmerber, Frankfurt am Main, 148 pp.
- Russ, G.R., 1984a. The distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. Marine Ecology Progress Series 20: 23-34.
- . 1984b. The distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Patterns of zonation on mid-shelf and outershelf reefs. Marine Ecology Progress Series 20: 35-44.
- Russell, B.C., 1983. Checklist of fishes Great Barrier Reef Marine Park Capricornia Section. Great Barrier Reef Marine Park Authority, Special Publication, Series (1), 184 pp.
- Russell, B.C. & A.M. Ayling, 1976. New records of fishes from northeastern New Zealand. Journal of the Royal Society of New Zealand 6(3): 277-286.
- Sauvage, H.E., 1880. Description de quelques poissons d'especes nouvelles de la collection du Muséum d'Histoire Naturelle. Bulletin de la Société Philomathique de Paris 4: 220-228.
- Seale, A., 1901. Report of a mission to Guam, Part 2: Fishes. Occasional Papers of the Bernice P. Bishop Museum 1: 61-128.
- . 1906. Fishes of the South Pacific. Occasional Papers of the Bernice P. Bishop Museum 4: 1-89.
- . 1909. New species of Philippine fishes. Philippine Journal of Science Section A, 4(6): 491-543.
- Smith, J.L.B., 1955a. The fishes of Aldabra. Part IV. Annals and Magazine of Natural History 12th Series, 8: 928-937.
- . 1955b. New species and new records of fishes from Mozambique. Memoir Museum Dr. Alvaro de Castro 3: 1-27.
- . 1956. The parrot fishes of the Family Callyodontidae of the western Indian Ocean. Ichthyological Bulletin Rhodes University 1: 1-23.
- . 1959. The identity of *Scarus gibbus* Rüppell, 1828 and of other parrotfishes of the Family Callyodontidae from the Red Sea and the Western Indian Ocean. Ichthyological Bulletin Rhodes University 16: 265-282.
- Schultz, L.P., 1958. Review of the parrotfishes, Family Scaridae. Bulletin of the United States National Museum 214: 1-143.
- . 1969. The taxonomic status of the controversial genera and species of parrotfishes with a descriptive list (Family Scaridae). Smithsonian Contributions to Zoology 17: 1-49.
- Steindachner, F., 1879. Ueber einige neue und seltene Fisch-Arten aus den K.K. Zoologischen Museum zu Wien, Stuttgart und Warschau. Denkschriften der Kais. Akademie der Wissenschaften, Wien 41: 1-52.
- . 1888. Ichthyologische Beiträge (XIV). Sitzber. Akademie der Wissenschaften, Wien 71: 123-168.
- Streets, T.H., 1877. Ichthyology: Fishes of upper and lower California. United States National Museum Bulletin 7: 43-102.
- Swainson, W., 1839. The Natural History of Fishes, Amphibians, and Reptiles, or Monocardian Animals.

- Volume 2. Longman, Orme, Brown, Green and Longmans, London, 392 pp.
- Taylor, W.R., 1964. Fishes of Arnhem Land. Records of the American-Australian Scientific Expedition to Arnhem Land 4: 45-307.
- Tosh, J.R., 1903. Marine biologists report. Notes on the habits, development etc., on the common food-fishes of Moreton Bay. Appendix to the Parlimentary Report of the Marine Department of Queensland for 1902-03: 17-24.
- Warner, R.R. & D.R. Robertson, 1978. Sexual patterns in the labroid fishes of the western Caribbean, I: The Wrasses (Labridae). Smithsonian Contributions to Zoology 254: 1-27
- Whitley, G.P., 1933. Studies in Ichthyology, No. 7. Records of the Australian Museum 19(1): 60-112.
- 1948. Studies in ichthyology, No. 13. Records of the Australian Museum 22(1): 70-94.
- 1964. Presidential address. A survey of Australian ichthyology. Proceedings of the Linnean Society of New South Wales 59: 11-127.
- 1966. Note on some Queensland fishes. Australian Zoologist 13(3): 235-243.
- Williams, D.McB., 1982. Patterns in the distribution of fish communities across the central Great Barrier Reef. Coral Reefs 1: 35-43.
- Williams, D.McB. & A.I. Hatcher, 1983. Structure of fish communities on the outer slopes of inshore, mid-shelf and outer-shelf reefs of the Great Barrier Reef. Marine Ecology Progress Series 10: 239-250.
- Woodland, D.J. & R.J. Slack-Smith, 1963. Fishes of Heron Island, Capricorn Group, Great Barrier Reef. University of Queensland Papers, Department of Zoology 2(2): 15-69.

Accepted 20 December 1985

PLATE 1

- 1A *L.vaigiensis* IP ♀
179 mm Mauritius
- 1C *C.spinidens* IP ♀
119 mm Negras,
Philippines
- 1E *C.carolinus* TP ♂
318 mm Honolulu
- 1G *C.bicolor* IP ♀
370 mm Guam
- 1I *H.longiceps* IP ♀
282 mm Rangiroa,
Tuamotu Islands
- 1B *L.vaigiensis* TP ♂
159 mm Mauritius
- 1D *C.carolinus* IP ♀
235 mm Honolulu
- 1F *B.muricatum* Adult ♂
510 mm Fanning Is.,
Line Islands
- 1H *C.bicolor* TP ♂
347 mm Takaroa,
Tuamotu Islands
- 1J *H.longiceps* TP ♂
303 mm Half Mile
Pass, GBR

PLATE 2

- 2A *S.rubroviolaceus* IP ♀
308 mm La Digue,
Seychelles
- 2C *S.gibbus* Red Phase ♀
393 mm Papeete, Tahiti
- 2E *S.psittacus* IP ♀
171 mm Lizard Is.,
GBR
- 2G *S.schlegeli* IP ♀
175 mm Tongtapu,
Tonga
- 2I *S.flavipectoralis* IP ♀
158 mm Alete Reef,
Solomons
- 2B *S.rubroviolaceus* TP ♂
355 mm Enewetak,
Marshall Islands
- 2D *S.gibbus* Green Phase
♂, 417 mm Teavaraa
Pass, Tahiti
- 2F *S.psittacus* TP ♂
228 mm Lizard Is.,
GBR
- 2H *S.schlegeli* TP ♂
240 mm Lizard Is.,
GBR
- 2J *S.flavipectoralis* TP ♂
206 mm Enewetak,
Marshall Islands

PLATE 3

- 3A *S.spinus* IP ♂
118 mm Heron Is.,
GBR
- 3C *S.chameleon* IP ♀
170 mm Lizard Is.,
GBR
- 3E *S.longipinnis* IP ♀
212 mm Pitcairn Is.
- 3G *S.pyrrhurus* IP ♀
117 mm Guadalcanal,
Solomons
- 3I *S.sordidus* IP ♀
164 mm Moorea, Tahiti
- 3B *S.spinus* TP ♂
144 mm Ponape,
Caroline Islands
- 3D *S.chameleon* TP ♂
209 mm Sumilon Is.,
Philippines
- 3F *S.longipinnis* TP ♂
193 mm One Tree Is.,
GBR
- 3H *S.pyrrhurus* TP ♂
220 mm Guadalcanal,
Solomons
- 3J *S.sordidus* TP ♂
227 mm Lizard Is.,
GBR

PLATE 4

- 4A *S.bleekeri* IP ♂
185 mm Fiji
- 4C *S.rivulatus* IP ♀
213 mm Lizard Is.,
GBR
- 4E *S.globiceps* IP ♀
166 mm Lizard Is.,
GBR
- 4G *S.oviceps* IP ♀
198 mm Teavaraa Pass,
Tahiti
- 4I *S.dimidiatus* IP ♀
192 mm Alete Reef,
Solomons
- 4B *S.bleekeri* TP ♂
200 mm Truk
- 4D *S.rivulatus* TP ♂
275 mm One Tree Is.,
GBR
- 4F *S.globiceps* TP ♂
222 mm Palmyra, Line
Islands
- 4H *S.oviceps* TP ♂
218 mm Alete Reef,
Solomons
- 4J *S.dimidiatus* TP ♂
189 mm Alete Reef,
Solomons

PLATE 5

- 5A *S.niger* Adult ♀
198 mm Enewetak,
Marshall Islands
- 5C *S.frenatus* IP ♀
217 mm Lord Howe Is.
- 5E *S.forsteni* IP ♀
249 mm One Tree Is.,
GBR
- 5G *S.ghobban* IP ♀
228 mm Ponape,
Caroline Islands
- 5I *S.altipinnis* IP ♀
262 mm Teavaraa Pass,
Tahiti
- 5B *S.frontalis* Adult ♂
350 mm Marcus Is.
- 5D *S.frenatus* TP ♂
234 mm Sudan, Red
Sea
- 5F *S.forsteni* TP ♂
252 mm Tahiti
- 5H *S.ghobban* TP ♂
255 mm Fanning Is.,
Line Islands
- 5J *S.altipinnis* TP ♂
234 mm Palmyra, Line
Islands

PLATE 6

- 6A *B.muricatum* Juvenile
105 mm Seribu Is.,
Java
- 6C *S.gibbus* Juvenile
59 mm Tahiti
- 6E *S.sordidus* Juvenile
37 mm Jana Is.,
Persian Gulf
- 6G *S.niger* Juvenile
45 mm Tahiti
- 6I *C.bicolor* Juvenile
100 mm Maldives
- 6B *H.longiceps* Juvenile
38 mm Port Moresby,
Papua New Guinea
- 6D *S.psittacus* Juvenile
43 mm Enewetak,
Marshall Islands
- 6F *S.altipinnis* Juvenile
47 mm Tahiti
- 6H *S.forsteni* Juvenile
41 mm Tutuila, Samoa
- 6J *S.frenatus* Juvenile
100 mm Lizard Is.,
GBR

PLATE 7

- 7A *S.gibbus* Juvenile
65 mm Enewetak,
Marshall Islands
- 7C *S.spinus* IP
140 mm Heron Is.,
GBR (D.R. Robertson)
- 7E *S.schlegeli* IP
185 mm Vava'u, Tonga
- 7G *S.schlegeli* Transitional
220 mm Lizard Is.,
GBR (A.M. Ayling)
- 7I *S.schlegeli* TP
200 mm Enewetak,
Marshall Islands
Central Pacific Variant
- 7B *S.gibbus* Green Phase
480 mm Enewetak,
Marshall Islands
- 7D *S.schlegeli* IP
110 mm Heron Is.,
GBR (D.R. Robertson)
- 7F *S.schlegeli* IP
210 mm Lizard Is.,
GBR (A.M. Ayling)
- 7H *S.schlegeli* TP
Lizard Is., GBR
(R. Kuiter)
- 7J *S.longipinnis* IP
165 mm Vava'u, Tonga

PLATE 8

- 8A *S.psittacus* Juvenile
50 mm Enewetak,
Marshall Islands
- 8C *S.psittacus* TP
Maldives
- 8E *S.sordidus* Juvenile
50 mm Lizard Is., GBR
- 8G *S.sordidus* TP
180 mm Lizard Is.,
GBR (A.M. Ayling)
- 8I *S.bleekeri* IP
Carter Reef, GBR
- 8B *S.psittacus* IP
150 mm Maldives
- 8D *S.psittacus* TP
Lizard Is., GBR
(R. Kuiter)
Reproductive
colouration
- 8F *S.sordidus* IP
150 mm Lizard Is.,
GBR
- 8H *S.sordidus* TP
Lizard Is., GBR
(R. Kuiter)
Reproductive
colouration
- 8J *S.bleekeri* TP
Lizard Is., GBR (R.
Kuiter)

Unless stated all photographs taken by the junior author. All lengths refer to Standard Length. All specimens from tank shots (Plates 1-6) deposited in the Bishop Museum.

PLATE 9

- | | |
|--|---|
| 9A <i>S.frontalis</i> Adult
240 mm Enewetak,
Marshall Islands | 9B <i>S.rubroviolaceus</i> IP
Lizard Is., GBR
(R. Kuiter) |
| 9C <i>S.rubroviolaceus</i> TP
550 mm Enewetak,
Marshall Islands
(Night) | 9D <i>S.chameleon</i> Juvenile
60 mm Lizard Is., GBR |
| 9E <i>S.chameleon</i> IP
160 mm Lizard Is.,
GBR | 9F <i>S.chameleon</i> IP
180 mm Lizard Is.,
GBR |
| 9G <i>S.chameleon</i> TP
Lizard Is., GBR
(A.M. Ayling) | 9H <i>S.chameleon</i> TP
Lizard Is., GBR
(R. Kuiter) |
| 9I <i>S.flavipectoralis</i> IP
190 mm Enewetak,
Marshall Islands | 9J <i>S.flavipectoralis</i> TP
240 mm Lizard Is.,
GBR |

PLATE 10

- | | |
|--|---|
| 10A <i>S.altipinnis</i> Juvenile
38 mm Tongtapu,
Tonga | 10B <i>S.altipinnis</i> IP
415 mm Enewetak,
Marshall Islands
(Night) |
| 10C <i>S.altipinnis</i> TP
470 mm Enewetak,
Marshall Islands | 10D <i>S.ghobban</i> IP
215 mm Kwajalein,
Marshall Islands |
| 10E <i>S.forsteni</i> IP
Lizard Is., GBR | 10F <i>S.forsteni</i> TP
Lizard Is., GBR |
| 10G <i>S.oviceps</i> Juvenile
95 mm Tongtapu,
Tonga | 10H <i>S.frenatus</i> IP
Seychelles |
| 10I <i>S.frenatus</i> TP
Seychelles | 10J <i>S.niger</i> Juvenile
50 mm Lizard Is., GBR |

PLATE 11

- | | |
|--|--|
| 11A <i>S.niger</i> Adult
240 mm Lizard Is.,
GBR | 11B <i>S.globiceps</i> IP
150 mm Heron Is.,
GBR (D.R. Robertson) |
| 11C <i>S.globiceps</i> TP
180 mm Half Mile Pass,
GBR | 11D <i>S.rivulatus</i> IP
Lizard Is., GBR
(R. Kuiter) |
| 11E <i>S.rivulatus</i> TP
Lizard Is., GBR
(A.M. Ayling) | 11F <i>S.rivulatus</i> IP
Lizard Is., GBR
Normal IP Colouration |
| 11G <i>S.rivulatus</i> IP
Lizard Is., GBR
Variant IP colouration | 11H <i>S.rivulatus</i> IP
Lizard Is., GBR
♀ Reproductive
colouration |
| 11I <i>S.rivulatus</i> IP
Lizard Is., GBR
IP ♂ Reproductive
colouration | 11J <i>S.rivulatus</i> TP
Lizard Is., GBR
TP ♂ Reproductive
colouration |

PLATE 1



A



B



C



D



E



F



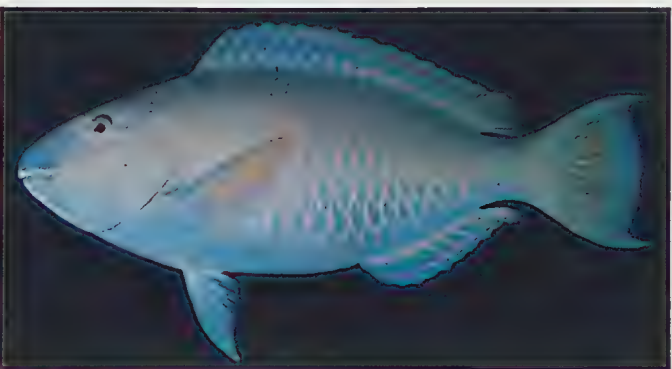
G



H



I



J

PLATE 2



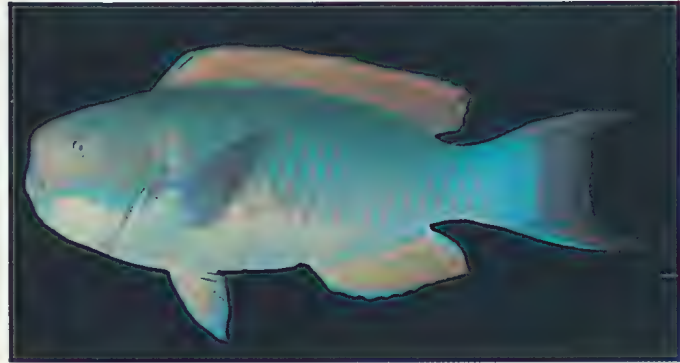
A



B



C



D



E



F



G



H



I

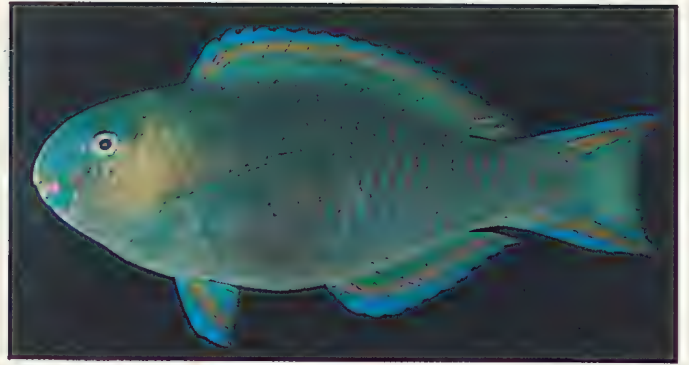


J

PLATE 3



A



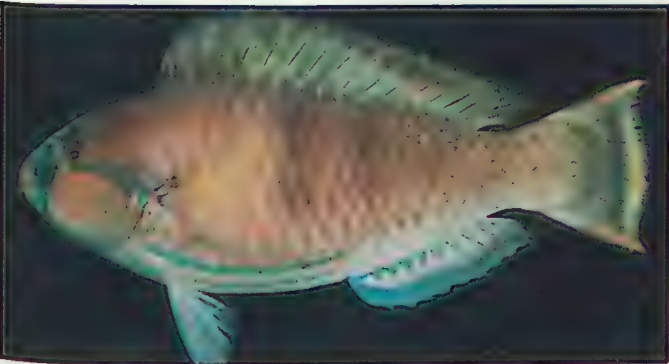
B



C



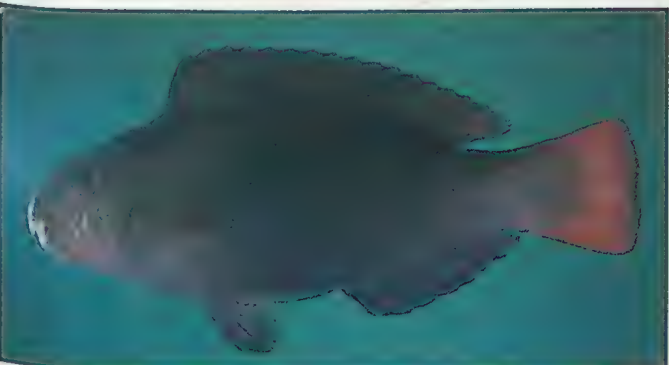
D



E



F



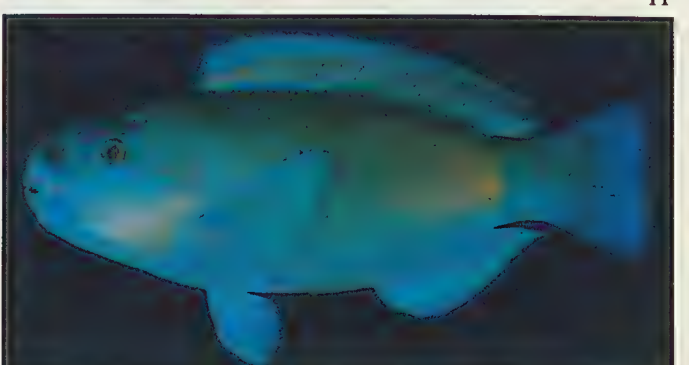
G



H



I



J



A



B



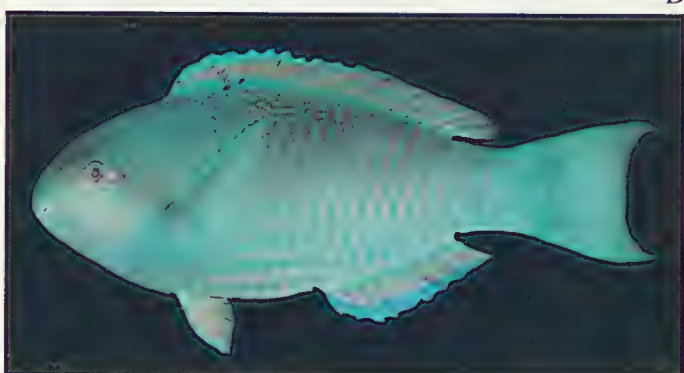
C



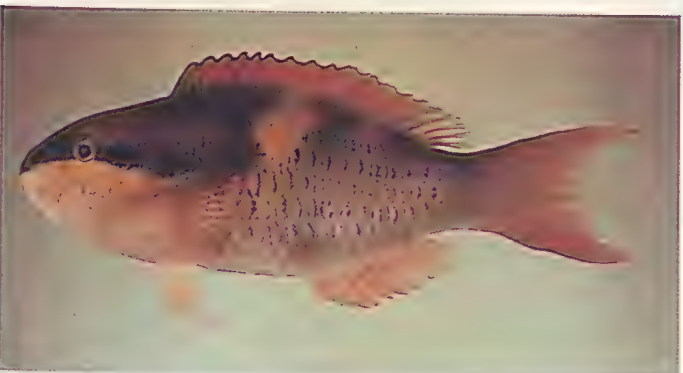
D



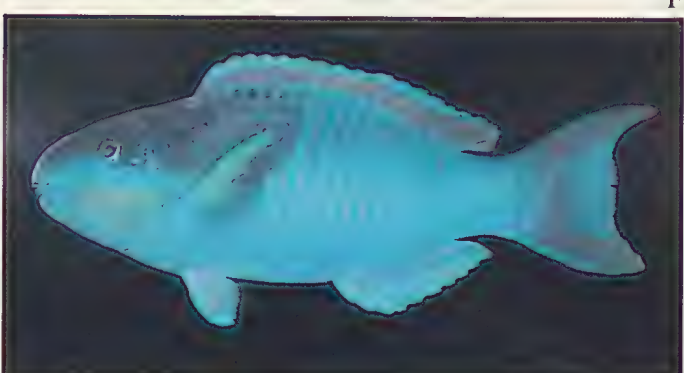
E



F



G



H

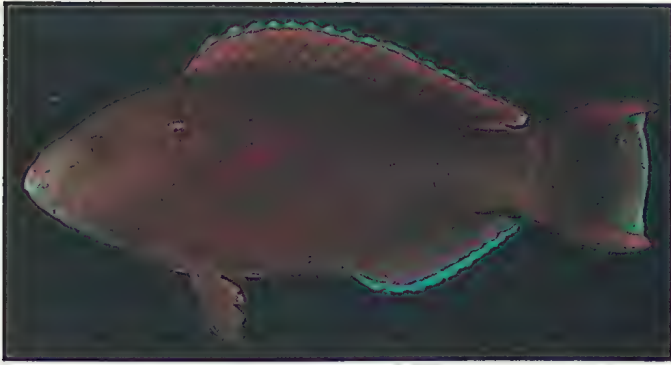


I



J

PLATE 5



A



B



C



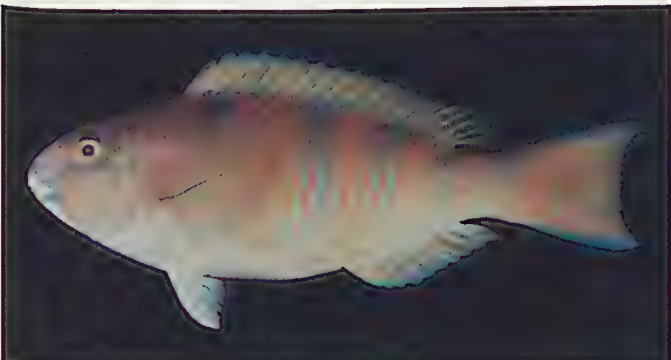
D



E



F



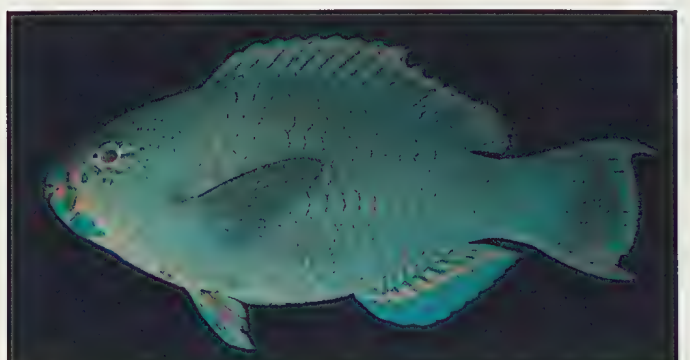
G



H

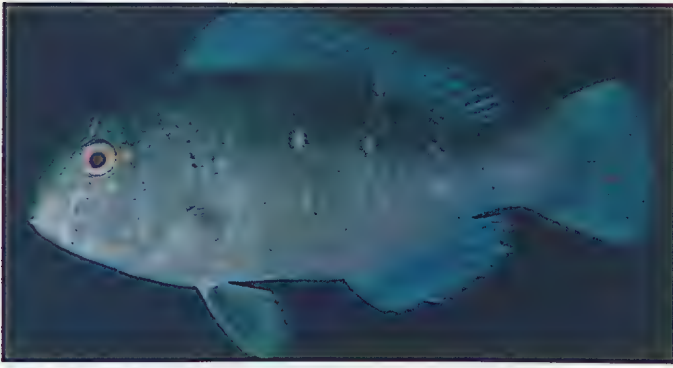


I



J

PLATE 6



A



B



C



D



E



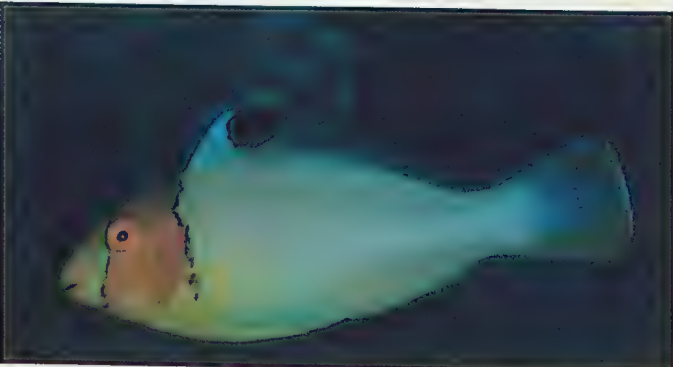
F



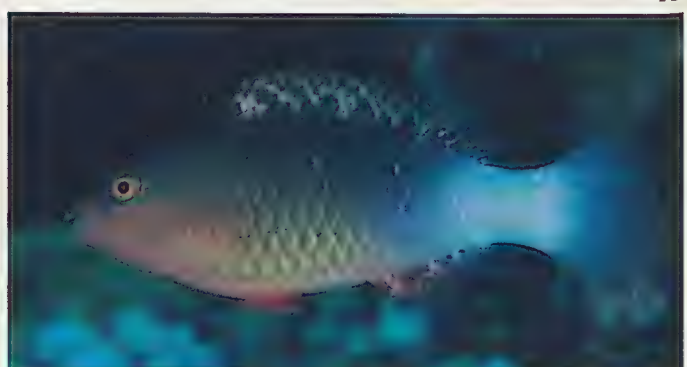
G



H



I



J

PLATE 7



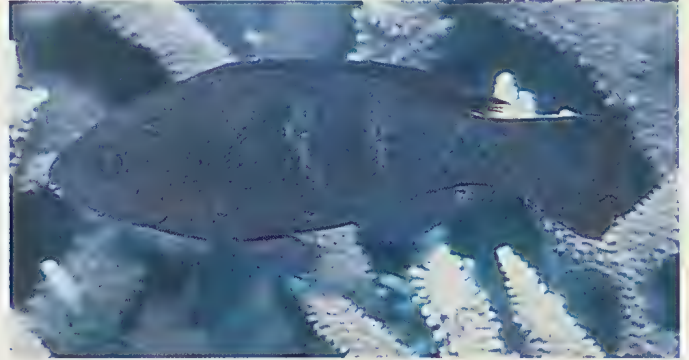
A



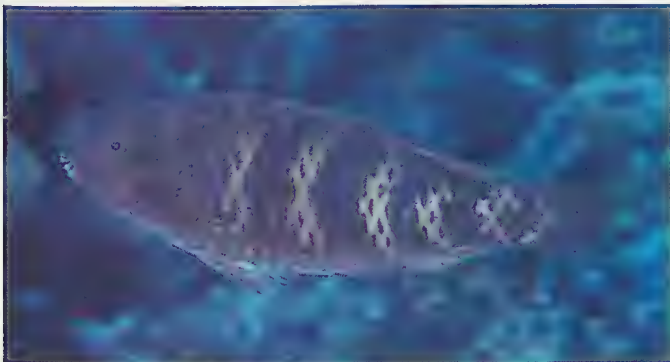
B



C



D



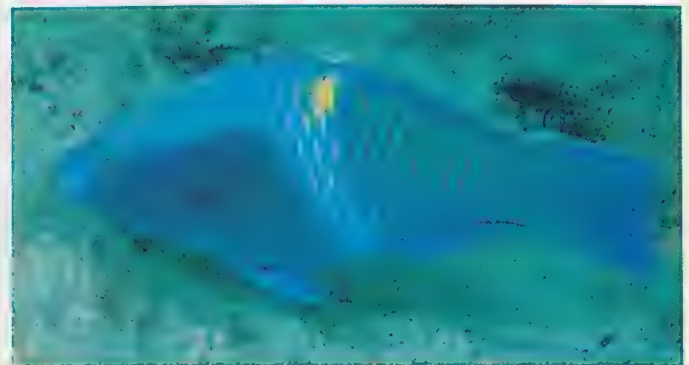
E



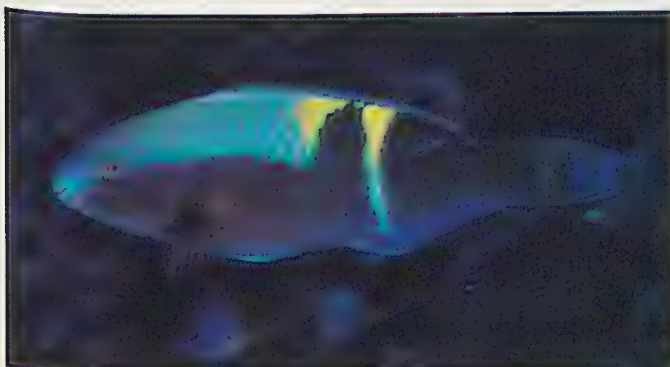
F



G



H



I

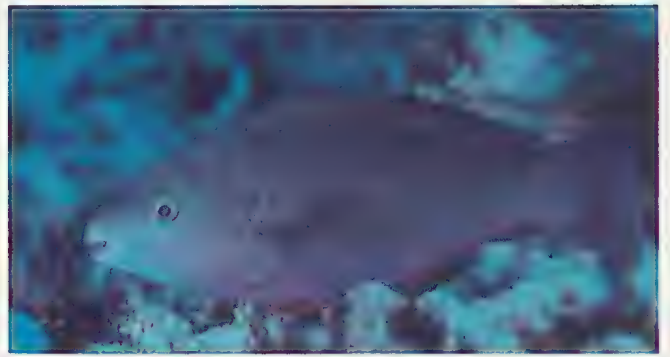


J

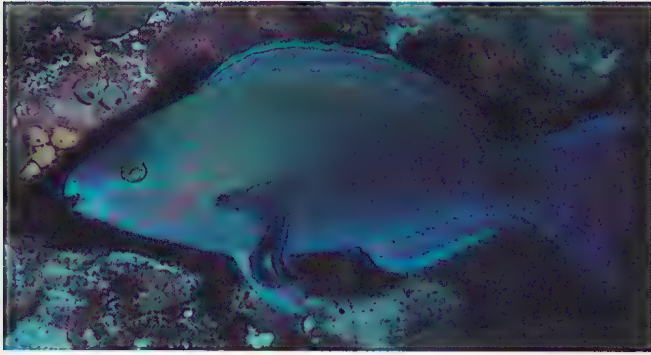
PLATE 8



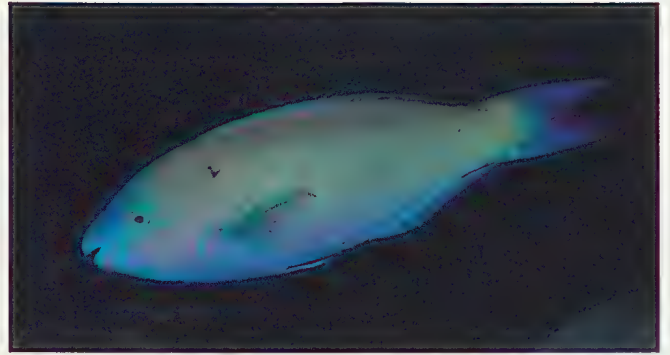
A



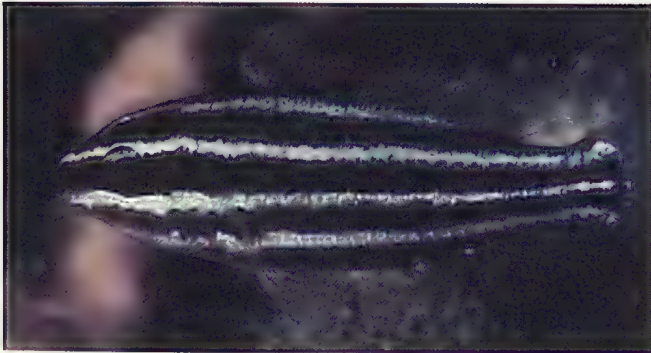
B



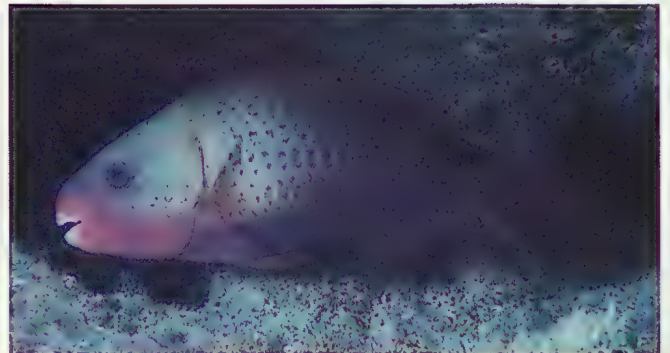
C



D



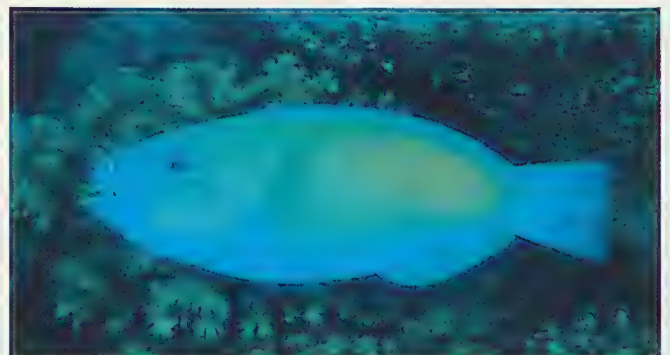
E



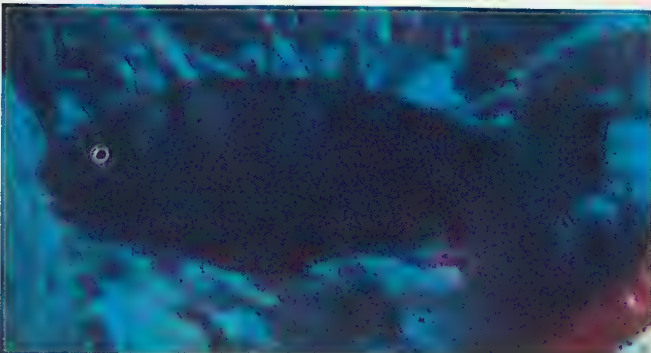
F



G



H

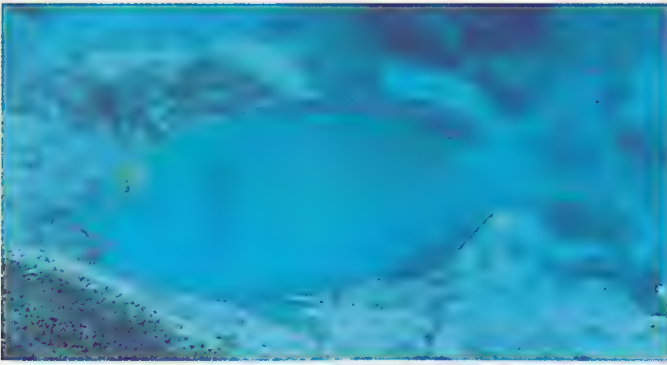


I

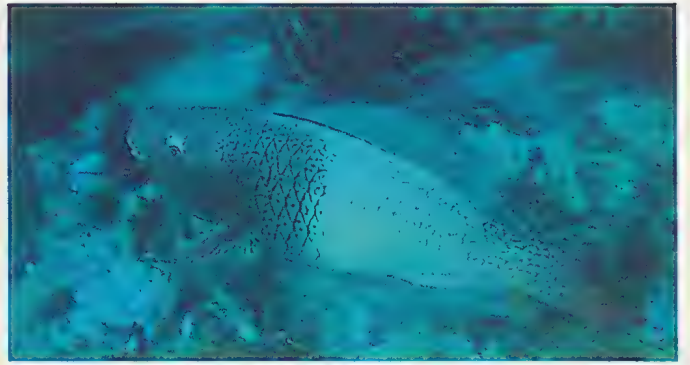


J

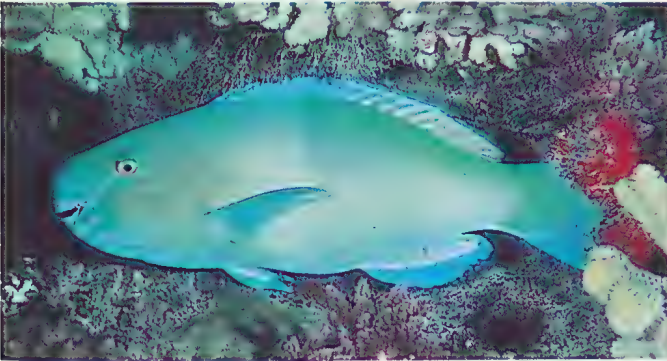
PLATE 9



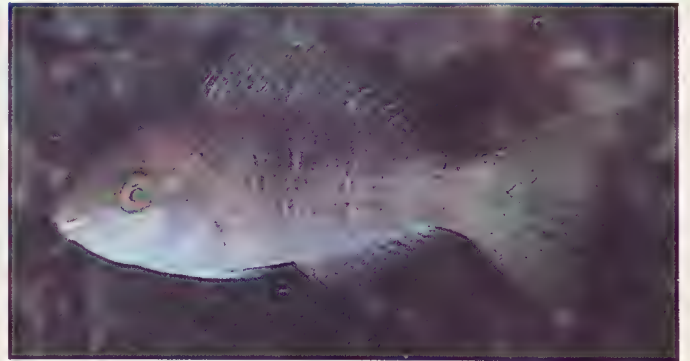
A



B



C



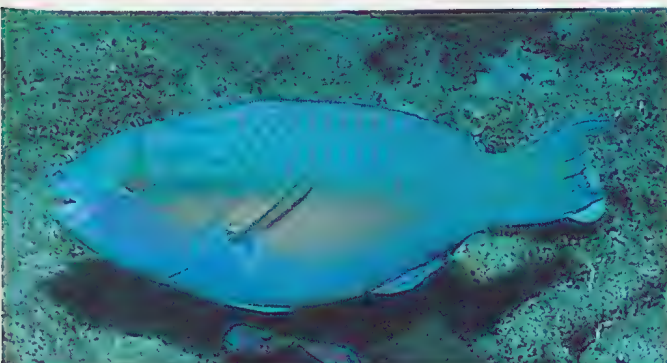
D



E



F



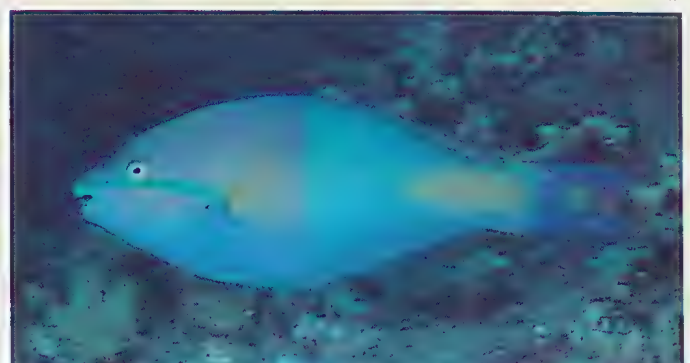
G



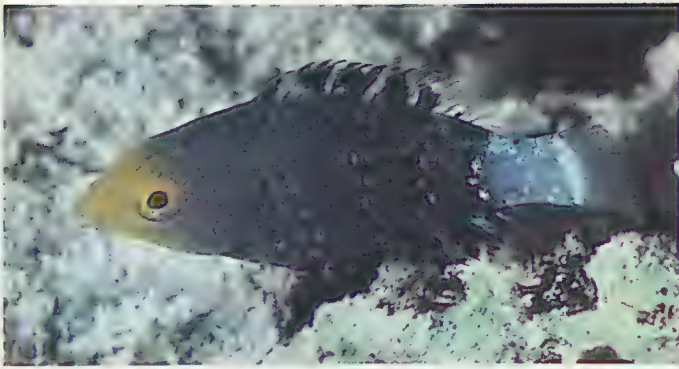
H



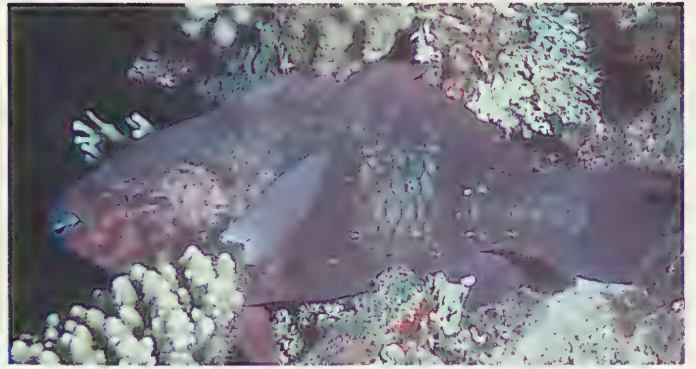
I



J



A



B



C



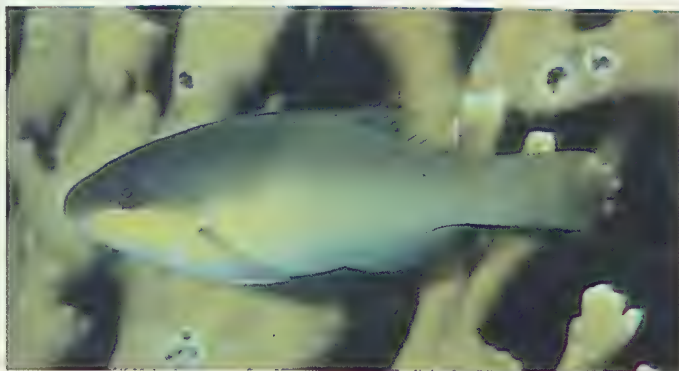
D



E



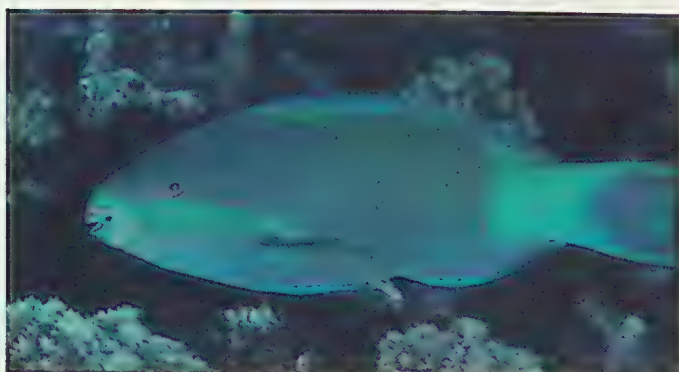
F



G



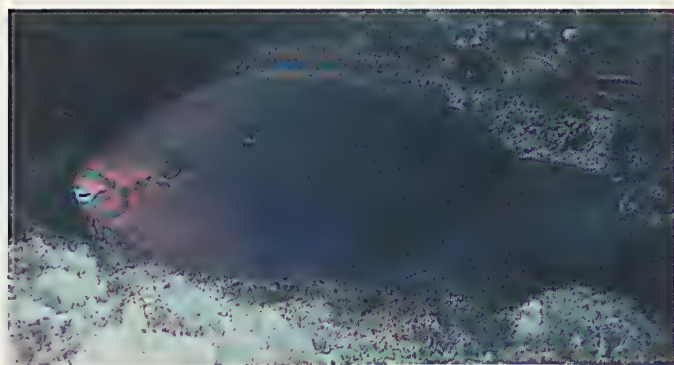
H



I



J



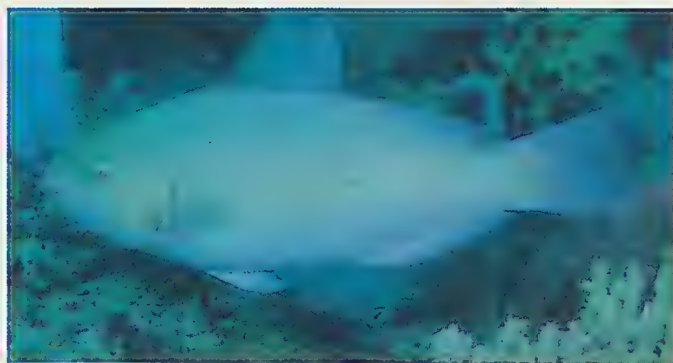
A



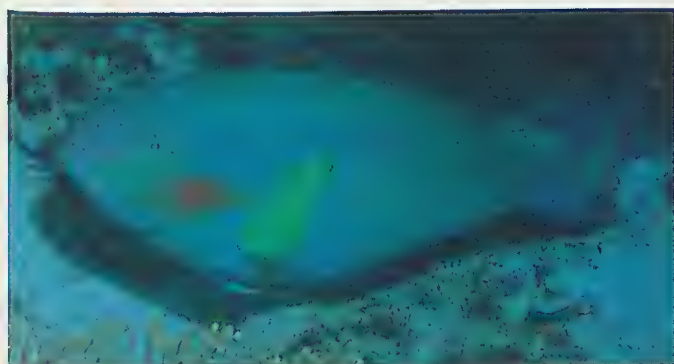
B



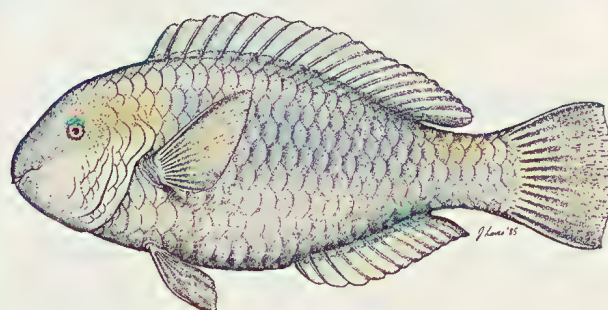
C



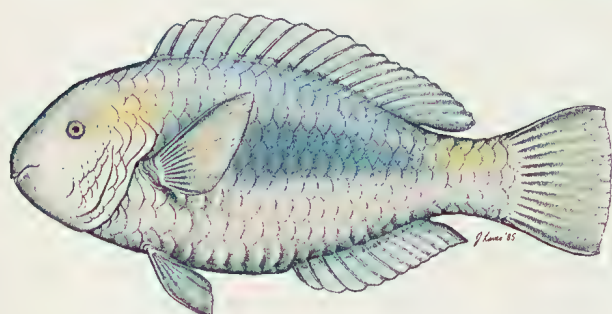
D



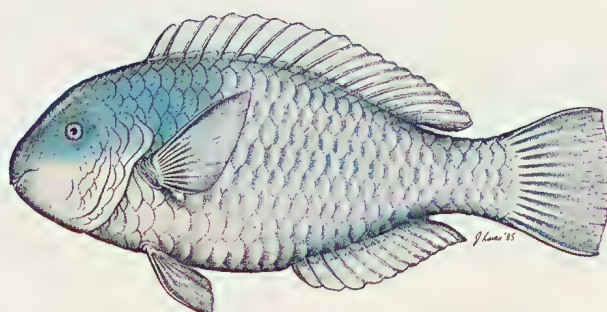
E



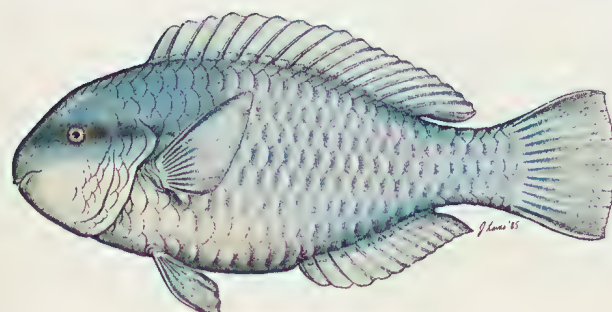
F



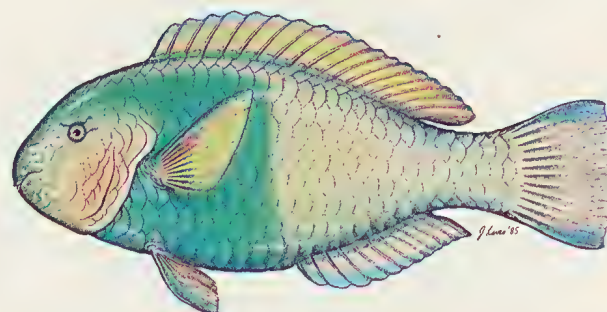
G



H



I



J

Review of the Types and Key to the Species of *Eunice* (Eunicidae: Polychaeta) from the Australian Region

KRISTIAN FAUCHALD

Department of Invertebrate Zoology, National Museum of Natural History,
Smithsonian Institution, Washington D.C. 20560, USA



ABSTRACT. Nineteen species of *Eunice* have been described from Australia, New Zealand and adjacent areas. The types of these species are redescribed and illustrated. Of the 19 species, two can no longer be recognized and no types are available. These two species, *E. gaimardi* and *E. quoya*, both described by Quatrefages (1866), are here considered indeterminable. A key to all species recorded from the area is given.

FAUCHALD, K., 1986. Review of the types and key to the species of *Eunice* (Eunicidae: Polychaeta) from the Australian Region. Records of the Australian Museum 38(5): 241-262.

About 30 species of *Eunice* have been identified from Australia and New Zealand (Day & Hutchings, 1979: 114-116); of these Day & Hutchings (1979) recognized 23 as valid. Nineteen species were originally described from Australia and New Zealand (cf. Hartman, 1959, 1965); the remaining species were originally described from other areas and subsequently recorded from New Zealand and Australia. Some taxa originally named from New Zealand and Australia that are often considered synonymous with other, widespread species, have been recognized as distinct in this paper. This brings the total known species from the region back up to 30. Most species of *Eunice* were described before the turn of the century, and have remained poorly known. This paper updates the description of all species originally named from Australia and New Zealand for which types were available. A complete treatment of the material deposited in the Australian Museum is in preparation, but cannot be completed until a revision of types of all species of *Eunice* has been performed. The world-wide revision will take several years to complete; members of the genus are important in ecological studies and a separate paper covering the species from this region will be useful to ecologists. A detailed discussion of the interrelations within *Eunice* must be postponed until all described species have been reviewed.

Standard illustrations and descriptions are given for all taxa available for examination and the separation

from related taxa is indicated. A key to all species currently recognized from the area is given. The character-set used to separate the species was discussed in detail by Hartman (1944) and Fauchald (1970); no additional characters have been added here.

Synonymies include only those that concern the type species examined. The often very brief original descriptions, usually without illustrations, has resulted in a very large number of incorrectly identified specimens. Without a complete review of the material on which these records were based, such synonymies would be more hindrance than help.

Scalemarks are 1 mm for all illustrations, except in all setal drawings in which the scalemarks are 0.1 mm.

ABBREVIATIONS

AM	Australian Museum, Sydney
BM(NH)	British Museum (Natural History), London
CM	Canterbury Museum, Christchurch
MNHN	Museum nationale d'Histoire Naturelle, Paris
MPW	Museum Przdonicze, Wroclaw
ZMH	Zoologisches Institut und Zoologisches Museum der Universitet, Hamburg
ZMB	Museum für Naturkunde, Berlin.

1	2	3	4	5	6	7	8	9	10
<i>E.aequabilis</i> *	Grube, 1878	C2	6	1	M	26,32	2	A	Number of branchial filaments decrease towards rear
<i>E.afra</i>	Peters, 1854	B4	18+	1	T	28,30	2	A	Maximally 5-6 branchial filaments
<i>E.afra paupera</i>	Grube, 1878	B4	20+	1	T	30	2	A	Maximally 1-2 branchial filaments
<i>E.antennata</i>	(Savigny, 1818)	C2	4-6	1	M	25	3	M	Decrease in numbers of branchial filaments in a median body region
<i>E.aphroditois</i>	(Pallas, 1788)	B2	5-7	1	T	35+	2	A	Summary description
<i>E.australis</i> *	Quatrefages, 1866	C1	7	1/3	T	31	2	A	Compound falcigers with blunt hoods
<i>E.bassensis</i> *	McIntosh, 1885	C2	?	(1)	T	?	2	?	Type incomplete
<i>E.bowerbanki</i> *	Baird, 1869	B2	5	1	T	31	2	M	Maximally 15 branchial filaments
<i>E.complanata</i> *	Grube, 1877	B4	19	1	T	28	2	S	Type dry; body cylindrical
<i>E.curticirris</i> *	Knox, 1960	B0	0	0	T	16	3	M	Type not seen; abbranchiate, subacicular hooks tridentate
<i>E.dilitata</i> *	Grube, 1856	B4	19	1	T	28	2	S	Body strongly flattened
<i>E.elseyi</i> *	Baird, 1869	C2	6	1	M	30	3	M	Number of branchial filaments decrease towards rear
<i>E.filamentosa</i>	Grube, 1856	B2	26	1	M	26	2	S	
<i>E.franklini</i> *	Monro, 1924	B2	6	1	T	34	2	A	Branchial filaments very short, numbering up to 25
<i>E.gracilis</i>	(Crossland, 1904)	B0	0	0	T	31	2	S	Abbranchiate, subacicular hooks bidentate
<i>E.grubei</i>	Gravier, 1900	B2	3	?	?	27	2	A	Maximally 8 branchial filaments
<i>E.indica</i>	Kinberg, 1865	C1	3	1/3	T	?	2	S	Compound falcigers with pointed hoods
<i>E.laticeps</i> *	Ehlers, 1868	B2	4	1	T	38	2	A	Maximally 18 branchial filaments
<i>E.longicirris</i>	Grube, 1869	B2	3	1	T	30	2	A	Maximally 8 branchial filaments
<i>E.makemoana</i>	(Chamberlin, 1919)	C2	7	1	T	28	2	M	All branchiae single filaments
<i>E.microprion</i>	Marenzeller, 1879	B2	4	1	T	33	2	A	Maximally 8 branchial filaments
<i>E.plicata</i> *	Baird, 1869	B2	7	1	T	25	2	A	Ventral cirri tipless
<i>E.pycnobranchiata</i> *	McIntosh, 1885	B2	6	1	T	28,29	2	A	Ventral cirri not inflated in median setigers
<i>E.rubella</i> *	Knox, 1951	B1	5	1/4	T	27	2	M	Type not seen
<i>E.torresiensis</i> *	McIntosh, 1885	C2	5	1	T	24	2	M	Numbers of branchial filaments decrease in a median region
<i>E.tribranchiata</i> *	McIntosh, 1885	B2	4,5	1	T	30	2	A	Ventral cirri scoop-shaped in median and posterior setigers
<i>E.tridentata</i> *	Ehlers, 1905	A1	3	1/2	T	51	2	A	
<i>E.tubifex</i>	Crossland, 1904	A4	35	1	T	29,32	2	S	Spinigers present
<i>E.vittata</i>	(delle Chiaje, 1828)	C1	3	1/3	T	16-24	2	A	Compound falcigers with pointed hoods

Table 1. Review of important morphological features of species of Eunice from Australia, New Zealand and adjacent areas. Species treated in detail are marked with an asterisk. The columns are: 1, species; 2, author; 3, species group *sensu* Fauchald (1970); 4, first occurrence of branchiae; 5, last occurrence of branchiae in fraction of the total body length; 6, shape of distal end of aciculae (M = modified, T = tapering); 7, first occurrence of subacicular hooks; 8, number of teeth in appendage of compound falcigers; 9, structure of antennae (A = cylindrical articulations, M = moniliform articulations, S = articulations absent); 10, remarks. ? in a column indicates missing information; parentheses indicates assumed condition.

TAXONOMY

Family EUNIDICAE Savigny, 1818

Eunice Cuvier, 1817

Prostomium with five antennae; peristomial cirri present. Maxillae include four pairs and one, unpaired MX III on the left side. Branchiae absent or present as single filaments or complex, pectinate structures. Setae including aciculae, subacicular hooks, pectinate setae and limbate setae. Aciculae and subacicular hooks translucent, yellow or light brown to black.

Type species. *Nereis aphroditois* Pallas, 1788 by subsequent designation (Hartman, 1959: 308).

Eunice aequabilis Grube, 1878

Figs 1-8

Eunice aequabilis Grube, 1878: 102.

Material examined. SYNTYPES: MPW 273 and ZMB 3993; Cape York, Australia, coll. Salmin (the label for the ZMB specimen suggests, incorrectly, that Grube collected the specimens).

Description. MPW syntype complete; 158 setigers; 175 mm long; 7 mm wide at setiger 15; length through setiger 10, 16 mm. ZMB syntype complete; 151 setigers; 183 mm long. Both syntypes flabby but otherwise in good condition.

Prostomium (Fig. 1) about $\frac{2}{3}$ peristomial width; anteriorly truncate. Eyes not visible. Outer lateral antennae reaching posterior end of first peristomial ring; inner lateral and median antennae reaching setiger 3; all antennae articulated; inner lateral and median antennae with 12 articulations; outer lateral antennae with 6 articulations. Peristomium nearly cylindrical; anterior ring $\frac{1}{2}$ of peristomial length; separation between rings well marked dorsally and ventrally, but not laterally. Peristomial cirri slender; reaching front edge of peristomium; with 5 articulations.

Jaws everted in ZMB syntype. Maxillary formula 1 + 1, 6 + 5, 8 + 0, 5 + 4 and 1 + 1. Mx III long; located behind left Mx II.

Branchiae (Fig. 2) from setiger 6 to end of body. All branchiae strongly pectinate; first branchia with 13 filaments; maximum 17 filaments at about setiger 20; number of filaments decreasing slowly posteriorly, but

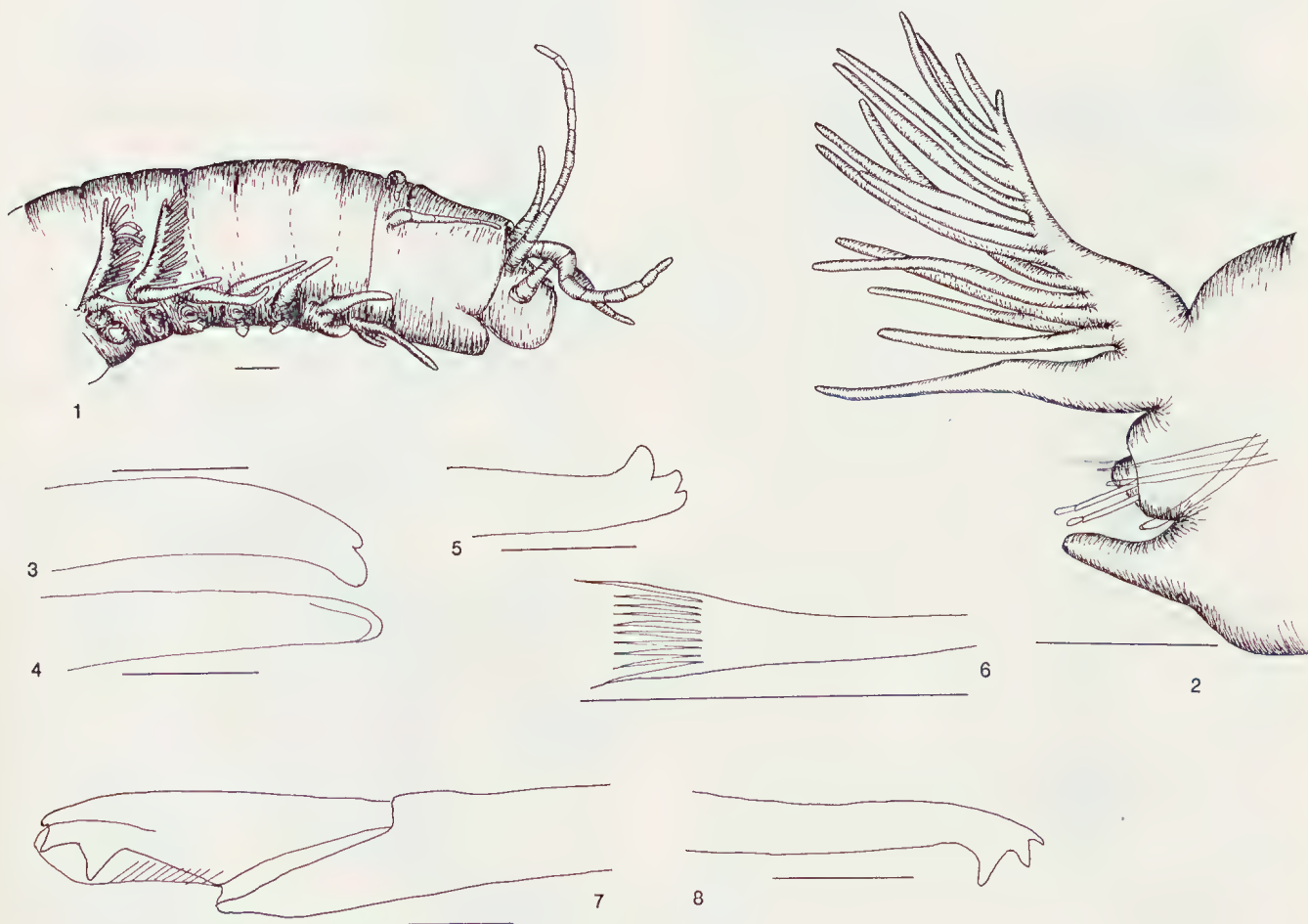
even in last segments 12 filaments present; median region with reduced numbers of filaments absent. Branchial stems conical; most filaments slender; about $\frac{2}{3}$ length of branchial stem in any segment. Branchiae never meeting in midline.

All acicular lobes (Fig. 2) distally obliquely truncate. Pre- and postsetal lobes low folds. Ventral cirri conical in first 3 setigers; thereafter basally inflated; inflated region decreasing posteriorly; by setiger 50 ventral cirri again conical; remaining conical in rest of body. Notopodial cirri basally inflated, in most setigers as long as branchial stems; articulations absent. Limbate setae marginally frayed, appearing brittle. Pectinate setae (Fig. 6) flat, tapering, with about 12 teeth; both marginal teeth longer than other teeth. Shafts of compound falcigers (Fig. 7) tapering evenly; appendages short, tridentate; proximal tooth largest; teeth decreasing evenly in size distally. Hoods short, distally rounded and marginally serrated. Aciculae (Fig. 4) yellow, paired; superior aciculae laterally flattened;

distally expanded into rounded tabs; inferior aciculae distally bidentate; dorsal teeth very much smaller than ventral teeth. Subacicular hooks (Figs 5, 8) yellow, tridentate; from setiger 26 in MPW syntype and from setiger 32 in ZMB syntype. Proximal teeth separated from 2 other teeth by distinct gaps.

Anal cirri long, slender with about 10 articulations.

Remarks. *Eunice aequabilis* belongs to the same group as *Eunice antennata* (C2, as defined by Fauchald, 1970) from which it appears to differ in that the branchiae retain a high number of branchial filaments in all setigers, in that the articulations on the long antennae are not moniliform and in the presence of a gap between the proximal and the 2 other teeth in the subacicular hooks. In *E. antennata* the number of branchial filaments decreases in a median region and increases again towards the posterior end; the antennae have moniliform articulations and the teeth of the subacicular hooks are evenly spaced.



Figs 1-8. *Eunice aequabilis* Grube (1878). 1, anterior end, lateral view; 2, parapodium 55 in anterior view; 3, acicula, parapodium 55, lateral view; 4, acicula, parapodium 55, ventral view; 5, subacicular hook, parapodium 55, lateral view; 6, pectinate seta, parapodium 134; 7, compound falciger, parapodium 134; 8, subacicular hook, parapodium 134. (Syntype, MPW 273.)

Eunice australis Quatrefages, 1866

Figs 9-14

Eunice australis Quatrefages, 1866: 321.*Eunice leuconuchalis* Benham, 1900: 21-22.**Material examined.** HOLOTYPE MNHN A1(R.)-1868-No.56a; New Zealand, coll. Quoy & Gaimard.**Description.** Holotype complete, in posterior regeneration; 109 setigers; last 10 in regenerate; 70 mm long; 4 mm wide; length through setiger 10, 9 mm.

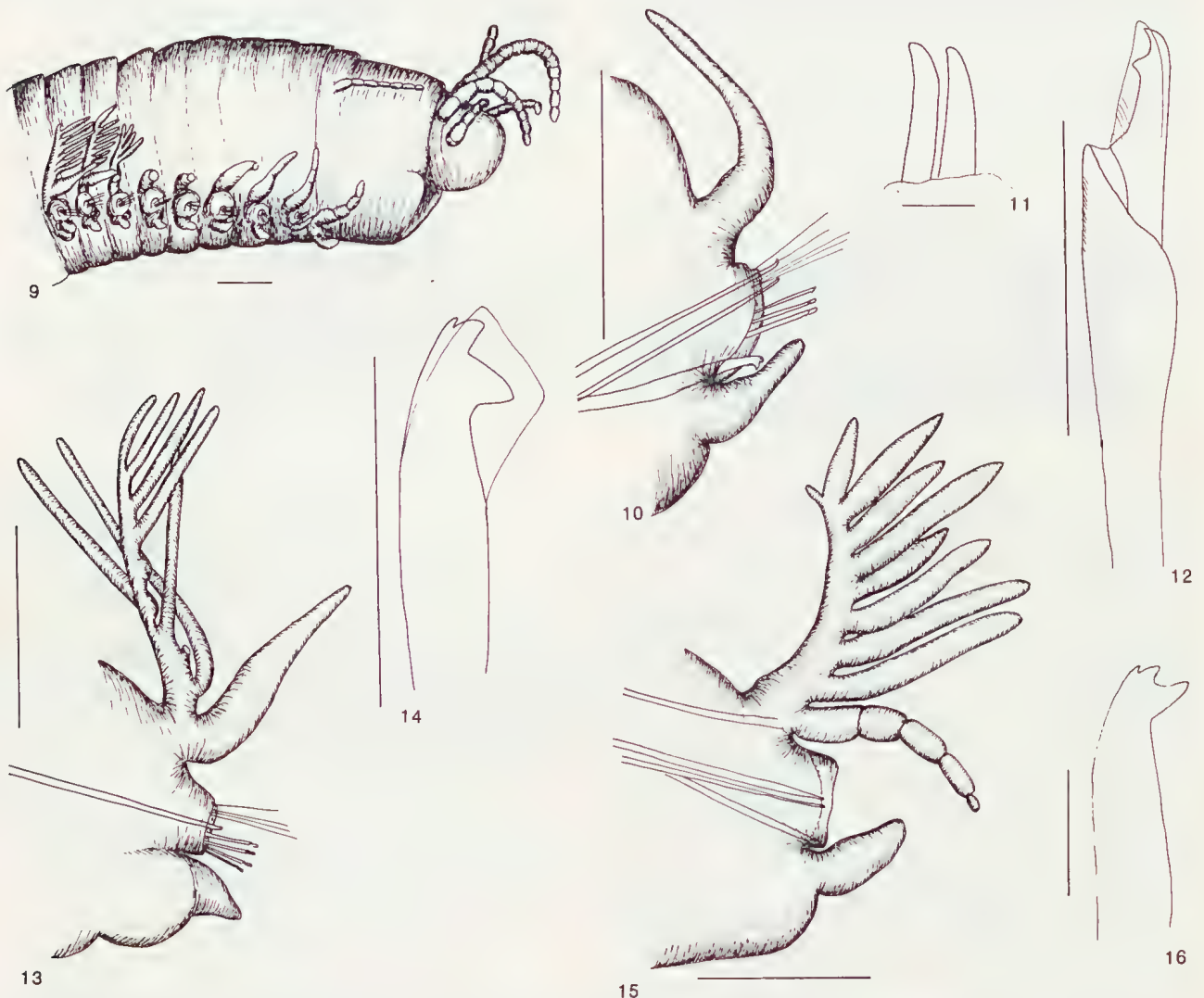
Prostomium (Fig. 9) 2 rounded lobes; nearly as wide as peristomium. All antennae articulated; articulations distinct, but not moniliform, except distally in median and inner lateral antennae; median antenna with 15 articulations. Outer lateral antennae reaching middle of peristomium; inner lateral antennae reaching setiger 1; median antenna reaching setiger 3. Separation between peristomial rings distinct dorsally and ventrally but not

laterally; anterior ring about $\frac{3}{4}$ of peristomial length. Peristomial cirri slender, not reaching anterior edge of peristomium; with 7 articulations.

Specimen ventrally dissected; maxillary formula 1 + 1, 6 + 6, 6 + 0 and 1 + 1. Mx III long; located behind left Mx II.

Branchiae (Fig. 13) from setiger 7 through 33; all except last 2 pairs pectinate; maximum number of filaments 8, at setiger 10.

Anterior parapodia (Fig. 13) distally truncate, becoming increasingly obliquely rounded posteriorly with high side dorsally (Fig. 10). Pre- and postsetal lobes low folds in all setigers. Ventral cirri digitiform in pre- and post-branchial setigers; basally inflated in branchial region. Prebranchial notopodial cirri digitiform; basally slightly inflated; with 2 long articulations. Notopodial cirri more distinctly inflated in branchial region, becoming increasingly slender in posterior setigers,



Figs 9-16. *Eunice australis* Quatrefages (1866). 9, anterior end, lateral view; 10, parapodium 68, anterior view; 11, acicula, parapodium 68; 12, compound falciger, parapodium 21; 13, parapodium 21, anterior view; 14, subacicular hook, parapodium 68; (MNHN, Paris, A1(R.) 1868-No. 56a). *Eunice bassensis* McIntosh, 1885. 15, parapodium 4, anterior view; 16, subacicular hook, parapodium 4. (Holotype, BM(NH) ZK 1885.12.1.207.)

remaining of similar length in all setigers. Limbate setae slender, marginally serrated. Pectinate setae tapering, flat; with about 12 teeth; both marginal teeth longer than other teeth. Shafts of compound hooks (Fig. 12) distally inflated; marginally finely serrated. Appendages short; relatively thick; bidentate; both teeth well developed; curvature of distal teeth varying somewhat in each fascicle, but teeth always distinctly curved, rather than erect. Hoods short; blunt with fine marginal serrations. Aciculae (Fig. 11) yellow, paired, distally tapered, bent dorsally. Subacicular hooks (Fig. 14) from setiger 31, yellow, tridentate, with large main fang and small secondary fang; third fang very small, closely appressed to secondary fang.

Remarks. *Eunice australis* has been widely reported from the Indian Ocean and the Southwest Pacific Ocean, but appears to have been confused with a number of similar species. Quatrefages had more than one specimen available, since he referred to the species as having 120–130 segments. The present specimen has 109. In other respects, Quatrefages' description is accurate, if somewhat incomplete. The relationships between *E. australis* and related species will be explored in detail elsewhere. It can be separated from other species reported from the region as indicated in the key and table. Justification for considering *E. leuconochalis* as a synonym is given in some detail below.

Eunice bassensis McIntosh, 1885

Figs 15–16

Eunice bassensis McIntosh, 1885: 298, pl. 39, fig. 16, pl. 21A, figs 8–9.

Material examined. HOLOTYPE: BM(NH) ZK 1885.12.1.207; off East Montcoeur Island, Bass Strait, 2 April 1874, 38–40 fms, dredged, sand, *Challenger* stn 162.

Description. Holotype anteriorly incomplete when first described; now consisting of 55 median and posterior setigers, last 22 plus pygidium in regeneration; 50 mm long; 3 mm wide.

Branched branchiae (Fig. 15) with relatively short filaments present; maximal number of filaments 9; continuing with 6–8 filaments through setiger 33; in regenerate 1–2 filaments per segment; branchiae present in all but last 2 or 3 setigers. Notopodial cirri (Fig. 15) with 3–4 distinctly marked articulations. Subacicular hooks (Fig. 16) in all setigers; yellow, tridentate. Compound falcigers bidentate. Hoods distally blunt. Aciculae yellow; distally tapering; bent.

Integument light coloured; containing numbers of white granules.

Remarks. The holotype appears to be the middle and last third of a very large specimen from which the head and at least 35 setigers are missing. Material identified as *E. bassensis* by Benham and resembling the type, is present in the collections of the Australian Museum, Sydney. These specimens were collected from the same geographical area and same habitat as the type. They

will be described in detail elsewhere.

Eunice bassensis was considered a junior synonym of *E. antennata* by Hartman (1959) and the features present in the type certainly resemble the conditions in that species. However, the notopodial cirri are very distinctly articulated in *E. bassensis* in median and posterior setigers and lack articulations in *E. antennata* in the same body region. The number of branchial filaments does not increase toward the posterior end in *E. bassensis* as it does in *E. antennata*; however, the regenerating condition of the posterior end of the type of *E. bassensis* may have confounded the development of the branchiae. The shape of the tridentate subacicular hook is distinctly different in the two species. *Eunice bassensis* is here considered valid despite the incomplete condition of the holotype.

Eunice bowerbanki Baird, 1869

Figs 17–23

Eunice bowerbanki Baird, 1869: 349–350.

Eunice bowerbanki.—Grube; 1878: 149.

Material examined. HOLOTYPE: BM(NH) ZH 1863.923.41; Australia, coll. Bowerbank.

Description. Holotype complete specimen in excellent condition; 142 setigers; 95 mm long; 7 mm wide; length through setiger 10, 11 mm.

Prostomium (Figs 17, 21) 2 well separated, spherical halves; distinctly narrower than peristomium. Inner lateral and median antennae reaching setiger 1; outer lateral antennae somewhat shorter. All antennae distinctly articulated; distalmost articulations moniliform; maximal number of articulations 8. Peristomium massive, especially ventrally (possibly through protrusion of jaws), dorsally divided into 2 rings; anterior ring $\frac{1}{2}$ of peristomial length. Peristomial cirri digitiform, not reaching frontal edge of peristomium, with 4 articulations.

Jaws (Figs 17, 21) everted. Maxillary formula 1 + 1, 4 + 4, 5 + 0, 5 + 8 and 1 + 1. Max III very small; closely appressed to left Max IV.

Branchiae (Fig. 18) from setiger 5–136. First branchia with 3 filaments; number increasing rapidly to maximum 15 by setiger 12. Number and length of filaments decreasing rapidly from setiger 18; by setiger 25 only 5–6 short, digitiform filaments left. Posterior $\frac{1}{2}$ of branchiated region with single filaments only.

Acicular lobes (Fig. 18) distally triangular, nearly symmetrical, supported by 1 or 2 acicula. Anterior postsetal lobes distally rounded, as high as setal lobe, becoming reduced to low folds by setiger 20. All presetal lobes low folds. Ventral cirri thick, digitiform in all setigers; basal inflated region poorly developed. Notopodial cirri basally supported by paired aciculae, increasing in length through setiger 4, then decreasing in length through next several setigers; by setiger 20 notopodial cirri no longer than branchial filaments. First few notopodial cirri digitiform, tapering evenly from

bases, with 2–3 articulations; next several cirri more pyriform, with distinct basal swellings decreasing posteriorly; by setiger 20, cirri thick, digitiform, lacking articulations, resembling branchial filaments in size and shape. Limbate setae slender. Pectinate setae (Fig. 23) short, slender, flat, flaring, with about 15 teeth; both marginal teeth somewhat thicker than other teeth, but not remarkably longer. Shafts of compound falcigers (Fig. 22) tapering; marginally smooth with internal oblique striations; appendages short, bidentate; distal teeth gently curved, more slender than proximal teeth. Hoods blunt, following outline of appendages closely. Aciculae (Fig. 19) black, single or paired; superior aciculae slender, tapering to straight tips; inferior aciculae thick, distally distinctly bent ventrally. Subacicular hooks (Fig. 20) from setiger 31, single or paired, black, bidentate, tapering smoothly toward tips; distal ends gently curved; teeth similar in size, both directed distally; hoods not observed.

Remarks. *Eunice bowerbanki* has not been reported since its original description, nor has it ever been illustrated. The species belongs to group B2 (Fauchald, 1970). It is differentiated from other species in the group by a combination of features including the beaded antennae, the bent acicular tips and the structure of the compound falcigers, with their nearly straight tips, in

addition to the reduction in size of Max III.

Eunice bowerbanki was described from Australian waters, no further locality information is available.

Eunice complanata Grube, 1877

Eunice complanata Grube, 1877: 529.

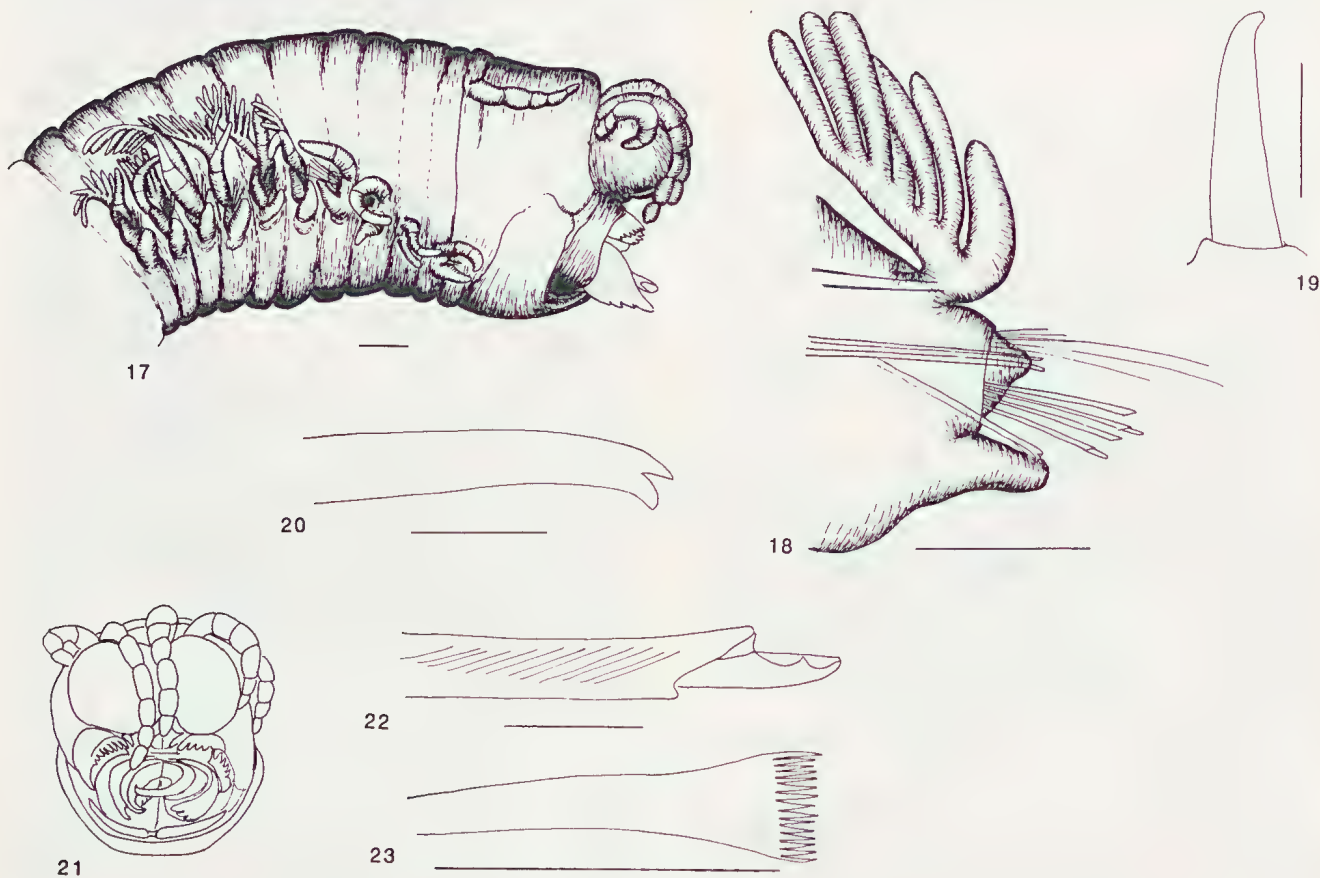
Material examined. HOLOTYPE: ZMB type 880, Timor, Atapupa and Salawatti, coral reef, dry.

Description. Holotype completely dry; incomplete; about 100 setigers; original reported length, 72 mm, apparently correct.

Prostomium completely shrunken; black eyes between inner and outer lateral antennae. Antennae perhaps reaching beyond tip of prostomium; apparently without articulations. Peristomial rings distinct dorsally and ventrally, but not laterally; anterior ring more than $\frac{5}{6}$ of peristomial length. Peristomial cirri at least as long as outer lateral antennae, apparently reaching well beyond frontal margin of peristomium, apparently without articulations.

Jaws half everted; maxillary formula 1+1, 5+5, 5+0, 4+8 and 1+1. Mx III short; part of distal arc with left Mx IV and V.

Branchiae from setiger 19, well developed on last



Figs 17–23. *Eunice bowerbanki* Baird, 1869: 17, anterior end, lateral view; 18, parapodium 34, anterior view; 19, acicula, parapodium 34; 20, subacicular hook, parapodium 34; 21, anterior end, frontal view; 22, compound falciger, parapodium 34; 23, pectinate seta, parapodium 34. (Holotype, BM(NH) ZM 1863.9.23.41.)

setigers present (setiger 100), with strong branchial stems; maximally 6 filaments. First 2 pairs single filaments only; all other branchiae pectinate.

Parapodia too distorted for adequate description. Ventral cirri basally inflated in some anteromedial segments; free tips distinct in all segments. Limbate and pectinate setae present. Compound falcigers bidentate. Aciculae and subacicular hooks dark. Aciculae tapering to points. Subacicular hooks from setiger 28; bidentate; rather thick.

Remarks. *Eunice complanata* belongs to group B4 (Fauchald, 1970); it resembles *E. afra* Peters (1854) in important respects, but the antennae appear to have been longer than usual in that species and the relation between the start of the branchiae and the subacicular hooks is also unusual for that group of species. It can be separated from other species reviewed in this paper by features indicated in Table 1.

Eunice curticirris Knox, 1960

Figs 24–28

Eunice (*Nicidion*) *curticirris* Knox, 1960: 125–126.

Material examined. HOLOTYPE: CM; Chatham Islands, 43°36.2'S, 176°48.5'W, south of the Sisters, 38 fms, coarse shell, sand, gravel, Chatham Islands Expedition stn 24.

Description. Holotype complete; 55 setigers; 12 mm long; 1 mm wide; length through setiger 10, 2.25 mm.

Prostomium (Fig. 24) large; frontally rounded lobe with longitudinal ventral groove. All antennae reaching setiger 1; consisting of 3 or 4 very large, angular articulations and short, ring-shaped ceratophores. Large, reddish eyes between bases of outer and inner lateral antennae. Peristomium about as long as prostomium, flaring, especially antero-ventrally;

separation between peristomial rings very distinct dorsally, less so ventrally and totally obscure laterally; anterior ring roughly $\frac{3}{4}$ of peristomial length.

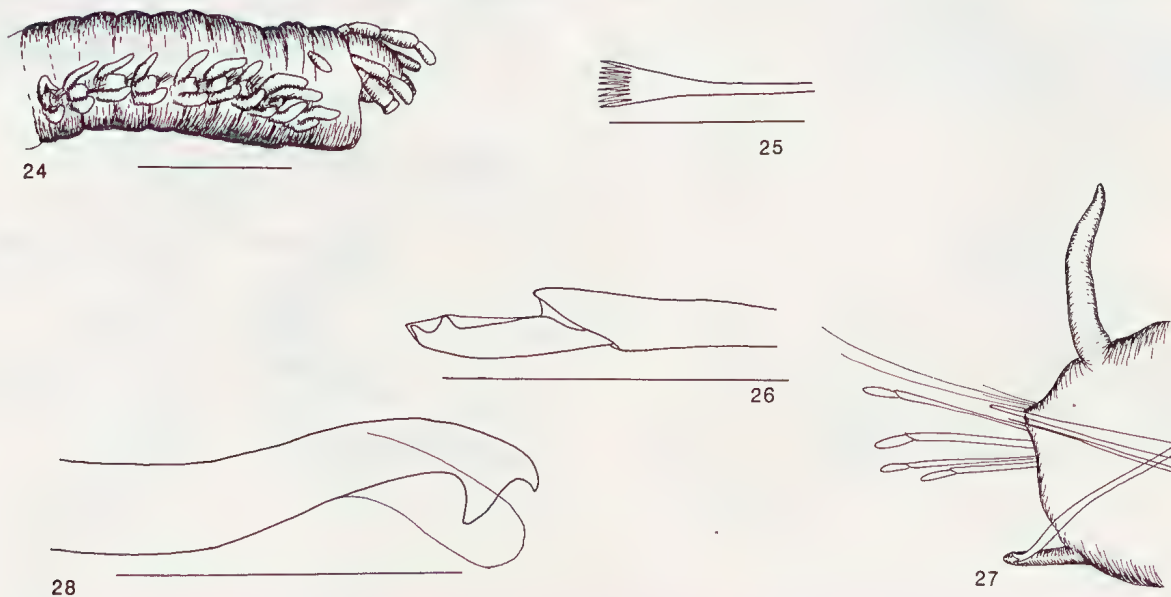
Peristomial cirri ovoid; reaching middle of peristomium.

Maxillary formula unknown.

Branchiae absent.

Acicular lobes of first 20 parapodia distinct and distally transverse; becoming reduced posterior to setiger 20 with aciculae emerging direct from the bodywall in posteriorly to setiger 25. Anterior notopodial cirri thick, Anterior ventral cirri thick, tapering, basally inflated from about setiger 12; retaining distinct, rounded tips, becoming tapering and nearly triangular in outline posterior to setiger 25. Anterior notopodial cirri thick, digitiform, becoming more slender posterior to setiger 20 (Fig. 27). Limbate setae slender. Pectinate setae (Fig. 25) tapering, flat, with about 10 teeth; marginal teeth no longer than other teeth. Shafts of compound hooks (Fig. 26) distally slightly inflated, marginally smooth; appendages bidentate; proximal teeth large, triangular; distal teeth well developed, angularly bent. Hoods distally bluntly and symmetrically truncate. Aciculae paired, black, smoothly tapering, distally pointed. Subacicular hooks from setiger 16, black, bidentate. Each hook (Fig. 28) distinctly S-shaped, with a tapering neck; distal and proximal teeth very large, curved; distal end nearly clear and translucent. No tridentate hooks observed.

Remarks. Knox (1960) mentioned that tridentate hooks with the distal tooth divided laterally were present in this species. No such hooks were observed in the specimen, but several parapodia are missing and such hooks could have been present in at least a few parapodia. *Eunice curticirris* can be separated from all other abbranchiate species of the genus by the extremely strongly beaded antennae.



Figs 24–28. *Eunice curticirris* Knox, 1960. 24, anterior end, lateral view; 25, pectinate seta, parapodium 35; 26, compound falciger, parapodium 35; 27, parapodium 35, anterior view; 28, subacicular hook, parapodium 35. (Holotype, CM.)

Eunice dilatata Grube, 1877

Figs 29–34

Eunice dilatata Grube, 1877: 530.**Material examined.** HOLOTYPE: ZMB 896: Salavatti, Timor, coll. S.M.S. Gazelle.**Description.** Holotype incomplete; 92 anterior setigers; 70 mm long; 5 mm wide at setiger 10; nearly 10 mm wide at posterior end of fragment; length through setiger 10, 16 mm. Anterior part of body cylindrical; body becoming strongly flattened with very short, crowded segments posteriorly.

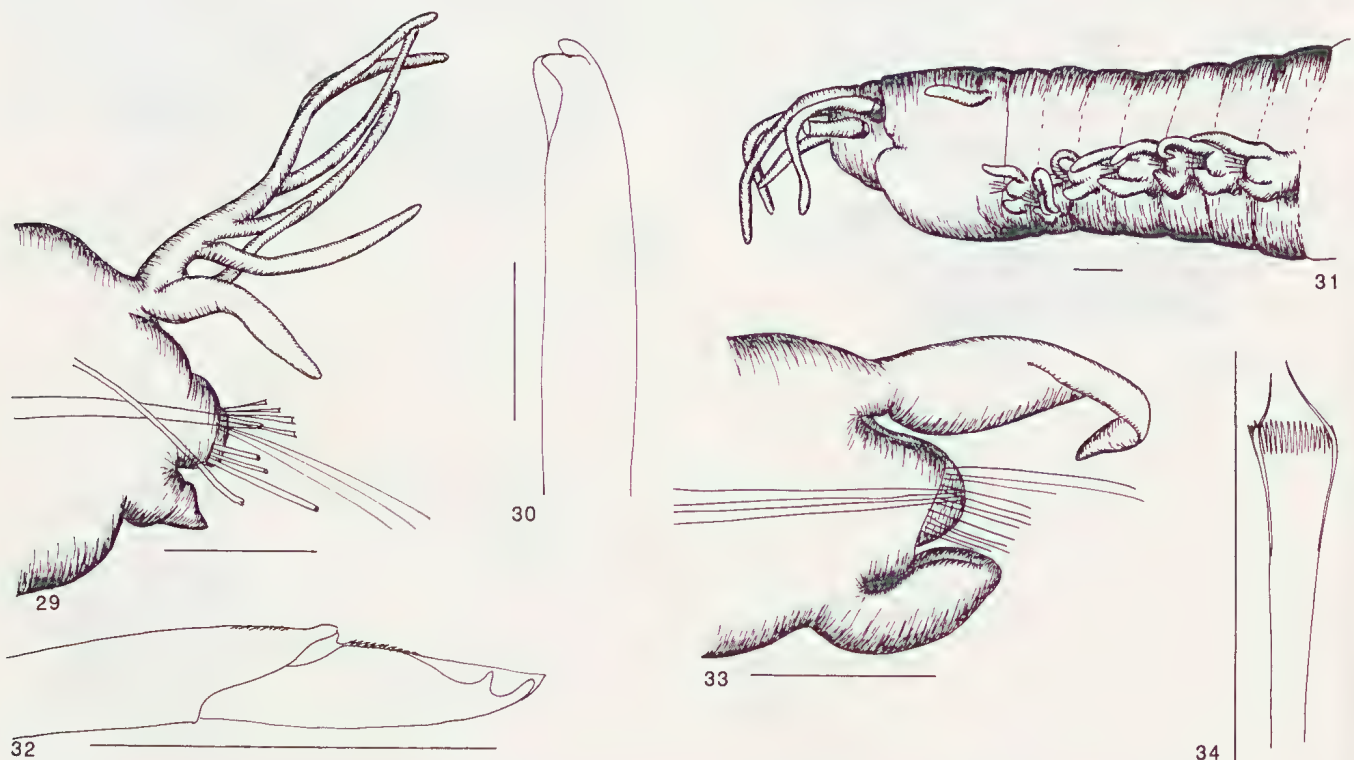
Prostomium (Fig. 31) 2 flattened lobes, well separated medially. Black eyes between bases of outer and inner lateral antennae. All antennae lacking articulations. Outer lateral antennae reaching second peristomial ring; inner lateral antennae reaching of setiger 1; median antenna reaching end of setiger 2; base of median antenna well forward of base of inner lateral antennae; median antenna about $\frac{1}{2}$ as wide as inner lateral antennae. Peristomium about twice as long as prostomium; separation between rings indistinct; visible only dorsally; anterior ring $\frac{3}{4}$ of peristomial length. Peristomial cirri short, digitiform.

Maxillary formula 1 + 1, 5 + 5, 8 + 0, 6 + 7 and 1 + 1; teeth of maxilla II unusually large and heavy. Mx III part of distal arc with left Mx IV and V.

Branchiae (Fig. 29) from setiger 19. First several pairs simple filaments; number of filaments increasing to maximum of 6; most branchiae with 5 filaments; this

number continuing to end of fragment. Filaments increasing in length posteriorly.

Anterior acicular lobes (Fig. 33) rounded; symmetrical; becoming distally transverse (Fig. 29) in median setigers. All presetal lobes low, obliquely transverse folds. Anterior postsetal lobes free, rounded, about as high as acicular lobes; becoming reduced to low folds in median setigers. Median and posterior parapodia carried on high ridges so that whole parapodial structure, including acicula are free of body wall, resembling large, flattened paddles with parapodial structure at distal end. Anterior ventral cirri large, tapering, folded over ventral edge of parapodia like a scoop. Ventral cirri basally inflated in branchial region, retaining rectangular free tips in all setigers. Anterior notopodial cirri pyriform, basally distinctly inflated with narrowed necks attaching to bodywall, decreasing in size in branchial region, remaining pyriform in all setigers. Limbate setae narrow, nearly capillary, in sparse dorsal fascicles. Pectinate setae (Fig. 34) narrow, tapering, furled, with about 15 teeth; both marginal teeth prolonged. Shafts of compound hooks (Fig. 32) smoothly tapering, marginally serrated; appendages large, bidentate, with both teeth similar in size and distinctly curved. Hoods distally blunt, marginally serrated. Compound hooks in thick fascicles in prebranchial region, decreasing in number posteriorly, in last segments only 4 or 5 hooks present in a parapodium. Aciculae dark yellow in anterior setigers; darkening to dark brown in last setigers; tapering to



Figs 29–34. *Eunice dilatata* Grube, 1877. 29, parapodium 81, frontal view; 30, subacicular hook, parapodium 81; 31, anterior end, lateral view; 32, compound falciger, parapodium 6; 33, parapodium 6, anterior view; 34, pectinate seta, parapodium 81. (Holotype, ZMB 896.)

smooth, sharp tips. Subacicular hooks (Fig. 30) from setiger 28, single in a parapodium, brown, bidentate, distally abruptly tapered; both teeth similar in size.

Remarks. The type has been laterally dissected so the lower outline of the peristomium has been reconstructed in Fig. 31.

The strongly flattened body and the large numbers of compound hooks in anterior setigers are features often present in the genus *Marphysa* as are the relatively light brown, rather than black aciculae and subacicular hooks. Other features, most importantly the presence of peristomial cirri, align the species with the genus *Eunice*.

Eunice dilatata belongs to group B4 (Fauchald, 1970). It resembles *E. afra* Peters (1854) in several important features, but differs from all species in the group by having the posterior end strongly flattened, and by having brown, rather than black, subacicular hooks. The shape of the subacicular hooks is also unusual in the group. All other species in the group have cylindrical, only slightly flattened bodies, and the subacicular hooks are black or dark brown throughout the body in large specimens.

Eunice elseyi Baird, 1869

Figs 35–40

Eunice elsyi (sic) Baird, 1869: 344.

Eunice elseyi.—McIntosh, 1885: 286.

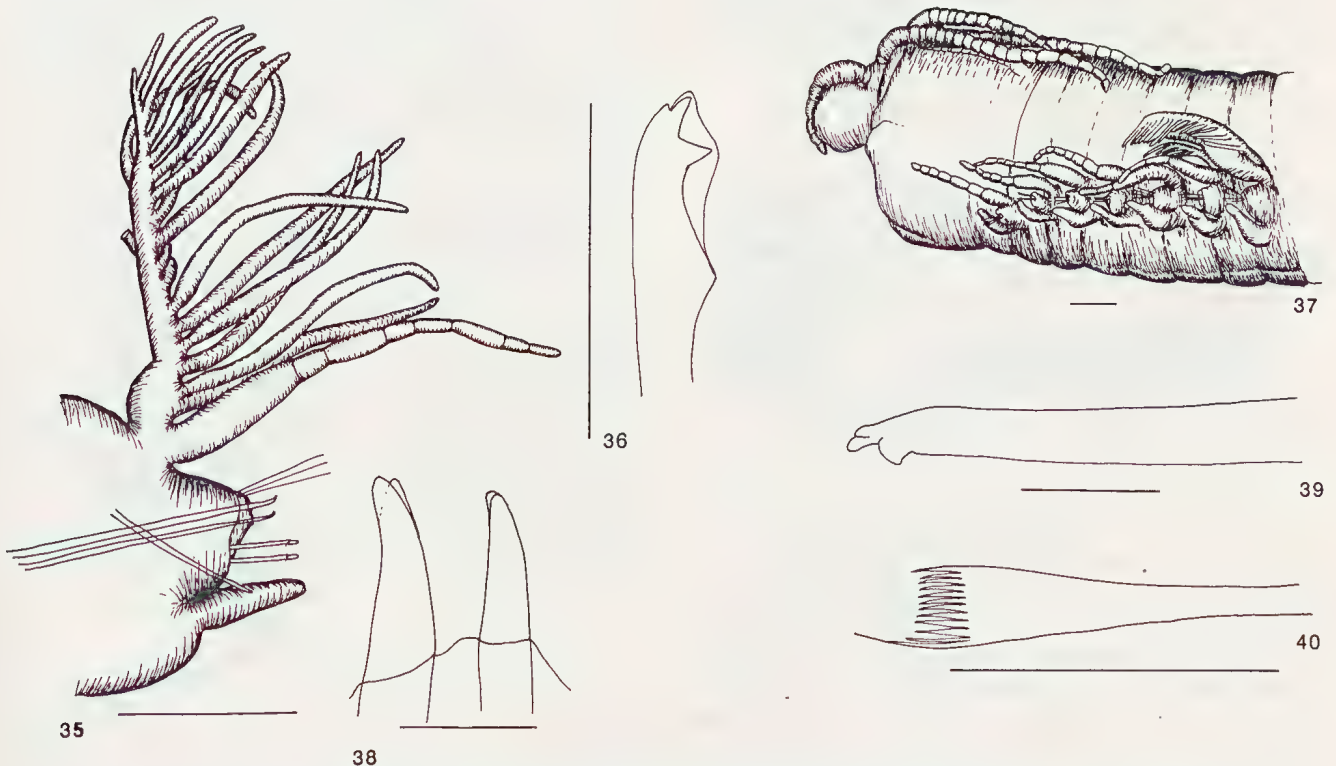
Material examined. SYNTYPE: BM(NH) ZH 1857.11.18.249; North Australia, coll. J.R. Elsey, North Australia Exploring Expedition, 1855–56. One specimen in 2 pieces, 2 mounted slides with parapodia and 1 slide with the jaws.

Description. Syntype complete; cut in 2 pieces; 120 segments; last 16 in regeneration; 64 mm long; 7 mm wide; length through setiger 10, 13 mm. Anterior end deeply dissected; jaws removed.

Prostomium (Fig. 37) 2 short, rounded lobes, well separated medially. All antennae strongly articulated with moniliform articulations; maximum number of articulations 22 in median antenna. Outer lateral antennae reaching posterior edge of first peristomial ring; inner lateral antennae reaching setiger 3; median antenna reaching setiger 5. Nuchal fold everted. Peristomium massive; separation between rings well marked ventrally, less distinct dorsally and missing laterally. Peristomial cirri slender, reaching frontal edge of peristomium; with about 10 articulations.

Jaws, presumably of syntype described, mounted on a slide; maxillary formula 1 + 1, 5 + 7, 6 + 0, 5 + 10 and 1 + 1. Mx III long; located behind left Mx II.

Branchiae (Fig. 35) from setiger 6; continuing to all but last 16 segments (in regeneration). All branchiae strongly pectinate; first branchia with 5 filaments; most other branchiae with at least 10 filaments; maximum 18. Branchial stems strong; erect; shortening posteriorly. Numbers of filaments high even in last segments; length of filaments decreasing posteriorly.



Figs 35–40. *Eunice elseyi* Baird, 1869. 35, parapodium 103, anterior view; 36, appendage of compound falciger, parapodium 103; 37, anterior end, lateral view; 38, both acicula, parapodium 103; 39, subacicular hook, parapodium 103; 40, pectinate seta, parapodium 103. (Holotype, BM(NH) ZH 1857.11.18.249.)

Acicular lobes (Fig. 35) distally transverse; pre- and postsetal lobes forming transverse folds. Ventral cirri digitiform in first 5 setigers, basally inflated, with distinct, digitiform tips in median setigers, becoming slender, digitiform in last branchiated segments. Notopodial cirri long, basally somewhat inflated, articulated in all segments except in regenerating portion, usually about as long as branchial stems, reaching nearly halfway across body. Limbate setae slender. Pectinate setae (Fig. 40) tapering, flat, with about 10 teeth; 1 marginal tooth longer than other. Shafts of compound hooks distally inflated; smooth; appendages (Fig. 36) distally tridentate; small third teeth closely appressed to second teeth. Aciculae (Fig. 38) yellow; distally bent towards dorsal side, distally shallowly bidentate in anteroposterior axis. Subacicular hooks (Fig. 39) from setiger 30, yellow, tridentate; main fang large; secondary fang small; third fang very small, closely appressed to side of secondary fang rather than emerging from back of hook.

Remarks. Another syntype in poor condition is present in BM(NH) (A. Muir, in litt.). The jaws and one parapodial slide fit with the specimen that is currently in good condition.

Baird referred to the aciculae as dark-coloured and specifically stated that no subacicular hooks (called uncini) were supposed to be present. The syntype has yellow aciculae and tridentate subacicular hooks. Combined with the presence of strongly moniliform antennae and tridentate compound hook, these features place the species in the same group as *Eunice antennata*, from which it can be separated on the high number of branchial filaments in the median segments and on the shape of the aciculae, which are bifid in *E. elseyi* and hammer-headed in *E. antennata*.

Another slide made of the parapodia, indicates that part of the original material belonged to a species with black, bidentate subacicular hooks and black, slender, tapering, bent aciculae. The segments, from which these parapodia had been removed, were branchiated, but the number of filaments cannot be accurately determined: the slide appears to have been compressed. However, the branchial stem was poorly developed and the number of filaments probably less than 10. These parapodia resemble those of species in group B2.

The specific name was spelled *elsyi* in Baird's original description, nevertheless he spelled the name of the collector correctly as Elsey at the end of the description. The label accompanying the type spells the name *elseyi* as did McIntosh (1885). It is here assumed that Baird's spelling of the specific name was a *lapsus calami* and that the corrected spelling of the name should be used.

Eunice franklini Monro, 1924

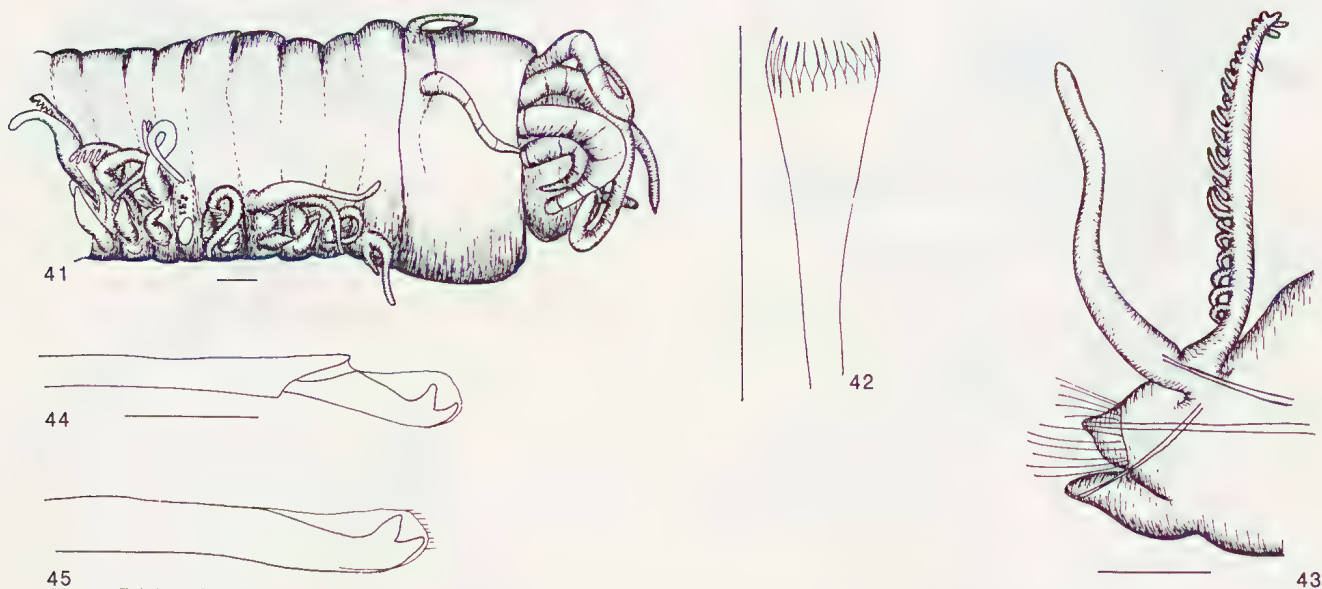
Figs 41–45

Eunice franklini Monro, 1924: 56–57, figs 14–16.

Material examined. HOLOTYPE: BM(NH) ZK 1924.1.28.81; the Franklin Shoal, Arafura Sea, 9°53'S, 129°19'E, one specimen, plus the jaws mounted on a slide.

Description. Holotype incomplete; frontally dissected; 92 setigers; 105 mm long; 7 mm wide; length through setiger 10, 15 mm.

Prostomium (Fig. 41) short, distinctly bilobed, narrower than peristomium. All antennae distinctly articulated; maximum 10 irregular articulations. Outer lateral antennae reaching setiger 1; inner lateral antennae (only left antenna intact) reaching setiger 4; median antenna reaching setiger 7. Separation between



Figs 41–45. *Eunice franklini* Monro 1924. 41, anterior end, lateral view; 42, pectinate seta, parapodium 69; 43, parapodium 69, anterior view; 44, compound falciger, parapodium 69; 45, subacicular hook, parapodium 69. (Holotype, BM(NH) ZK 1924.1.28.81.)

peristomial rings distinct dorsally; indistinct ventrally and laterally; anterior ring $\frac{1}{2}$ of peristomial length. Peristomial cirri tapering, more slender than antennae, similar in length to outer lateral antennae, with 5 indistinct articulations.

Jaw apparatus mounted separately; maxillary formula 1 + 1, 6 + 6, 8 + 0, 6 + 8 and 1 + 1. Mx III part of distal arc with left Mx IV and V.

Branchiae (Fig. 43) from setiger 6; continuing to end of fragment; all branchiae distinctly pectinate with very short, digitiform branchial filaments; maximum 27 filaments. Branchial stems well developed; shorter than notopodial cirri in most setigers.

Acicular lobes (Fig. 43) triangular with pointed area surrounding projecting aciculae. In first 15 setigers pre- and postsetal lobes distinct and free; rounded; thereafter reduced to transverse folds. Ventral cirri tapering towards blunt tips in all setigers; basal inflated region present, but indistinct. Notopodial cirri very long, basally supported by prominent aciculae, pyriform, longer than branchial stems in most segments. Limbate setae slender, marginally serrated. Pectinate setae (Fig. 42) flat, tapering, with about 12 teeth; both marginal teeth slightly longer than other teeth. Shafts of compound hooks (Fig. 44) slender, smoothly tapering, without distinct ornamentation; appendages short, slender, bidentate; distal teeth slightly slimmer than proximal teeth. Hoods distally rounded. Aciculae black, tapering evenly from base, distally straight. Two of 4 notopodial aciculae black; other 2 translucent. Subacicular hooks (Fig. 45) from setiger 34, black, bidentate; both teeth similar in size, covered by short, blunt hood.

Remarks. *Eunice franklini* remains known only from the type specimen which is incomplete, but the development of the branchiae indicate that most of the posterior segments must have been branchiated. The number of branchial filaments is reduced towards the posterior end, but even in the last setiger present 17 short branchial filaments are present. Judging from the tapering of the body, it appears that less than 50 segments are missing from the body and unless the branchial distribution is vastly different from the normal pattern in the genus, the species can be assumed to retain branchiae into the far posterior setigers. The species must belong to group B2 as defined by Fauchald (1970).

The relationship to similar species from Australian waters is indicated in the Key and Table 1. The combination of numerous very short branchial filaments and extremely long notopodia is unique to the genus.

Eunice gaimardi Quatrefages, 1866

Eunice gaimardi Quatrefages, 1866: 321.

Remarks. No material is available of this species in the MNHN (J. Renaud-Mornant, in litt.). The species was described by Quatrefages (in Latin, K. Fauchald translation with updated terminology) as follows: "The

prostomium is shallowly incised. The antennae are nearly moniliform. The peristomium is somewhat elongated. Short, indistinctly articulated peristomial cirri. Superior maxillae slender, inferior ones with 6 teeth. Teeth rounded. The mandible curved, shallowly incised frontally. Body with 120 segments. Notopodial cirri long and thick, ventral cirri very short. Branchiae with six branchial filaments."

Quatrefages' comments (in French, translation with updated terminology) read: "This species, reported by Quoy & Gaimard, is represented only by a single individual in rather poor state of preservation. The prostomium is shallowly incised. The median antennae are missing. The outer ones are nearly moniliform. The peristomium is as long as the next 3 segments together. The peristomial cirri are short and indistinctly articulated. The upper jaws are slender, the lower jaws have 6 small teeth. The margins of the jaws are undulating rather than denticulated. The mandible is straight and only a little incised. The body, which is incomplete, is 90 mm in length and consists of about 120 segments. The parapodia do not protrude much. The notopodial cirrus is thick and moderately long; the ventral cirrus is very small. The neuropodium, conical and distinct, carries compound setae in which the appendage has a large smooth tooth at the base of the spoon (?) and two strong teeth distally. Branchiae are first present from the sixth segment and have only six filaments."

The information is not sufficient to allow identification of the species and *E. gaimardi* is here considered indeterminable.

Eunice laticeps Ehlers, 1868

Figs 46–50

Eunice laticeps Ehlers, 1868: 312.

Eunice tentaculata Quatrefages, 1866: 317.

Material examined. HOLOTYPE of *E. tentaculata* Quatrefages, MNHP A1(R.)-1868-No. 52b; Port Western, Australia, coll. Quoy & Gaimard, 1839.

Description. Holotype of *E. tentaculata* incomplete; in 3 fragments. In addition a small posterior fragment with a pygidium present; its relation to holotype undetermined. Other fragments comprising 81 segments; 126 mm long; 10 mm wide; length through setiger 10, 21 mm. Anterior fragment with pro- and peristomium and first 38 setigers.

Prostomium (Fig. 46) has 2 massive rounded lobes, well separated medially. Antennal bases overlapped by overhanging nuchal fold. All antennae digitiform. Inner lateral and median antennae reaching middle of second peristomial ring; with 10 distinct, but not moniliform articulations. Outer lateral antennae reaching middle of first peristomial ring. Left outer lateral antenna doubled and left inner lateral antenna missing. Peristomium massive; separation between rings distinct dorsally, and visible ventrally, missing laterally. Peristomial cirri

short, slender; with 6 articulations.

Jaws halfway everted. Maxillary formula (as far as determinable) 1+1, ?4+?, 6+0, 6+9 and 1+1. Mandibles massive, strongly calcified, very friable. Mx III short; part of distal arc with left Mx IV and V.

Branchiae (Fig. 47) from setiger 4 to end of fragments. All branchiae pectinate; first branchia with 4 filaments; maximum number 18 at about setiger 20; most median segments with 10 or fewer filaments.

Acicular lobes (Fig. 47) distally truncate, with distinct steps from dorsal sections supported by aciculae to ventral, lower sections. Pre- and postsetal lobes low folds. Ventral cirri digitiform in anterior setigers; becoming basally inflated in branchial region; basal inflation less distinct in posterior fragments; ventral cirri more distinctly digitiform than in early branchial region. Anterior notopodial cirri digitiform; with 2 or 3 articulations, losing articulations posteriorly. Limbate setae narrow; marginally smooth. Pectinate setae (Fig. 48) usually at least 10 per segment, flat, flaring, with 15–20 teeth; 1 marginal tooth longer than other. Shafts of compound hooks (Fig. 49) tapering, marginally smooth, internally distinctly striated; appendages narrow, bidentate, with small proximal and distal teeth. Hoods short, blunt (not illustrated). Subacicular hooks (Fig. 50) from setiger 38; mostly singly, sometimes paired, black, bidentate, tapering; proximal teeth distinctly larger than distal teeth.

Remarks. The combination *Eunice tentaculata* was published by Kinberg (1865: 562) in a paper issued early in the year 1865. Quatrefages published his systematic scheme, including a revision to the generic level, but no species, in March, 1865 (Quatrefages, 1865a). This preview was reviewed by Claparède (anonymously, in April 1865) and the review led to a later rebuttal, and

reiteration of the same scheme by Quatrefages (1865b). Quatrefages' completed volumes, including the description of species was not issued until 1866, despite the date on the title page of the first volume (Wright, 1866: 578). The name *E. tentaculata* Quatrefages is thus a junior homonym, as Ehlers (1868: 312) noted in a footnote in which he re-named the species, without seeing any specimens and without adding anything to the description.

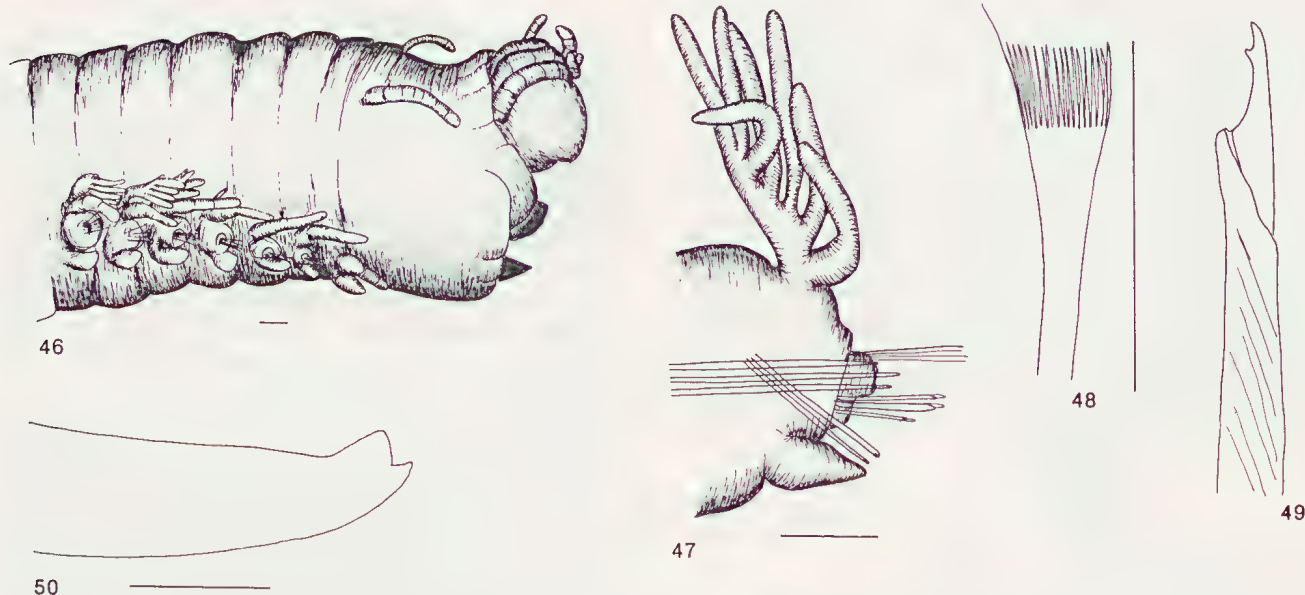
The issue was confused by Grube (1878: 99) who proceeded to replace *E. tentaculata* Kinberg with *E. valenciennesi*, on grounds of the supposed preoccupation of the combination; Hartman (1948: 76) accepted Grube's replacement name in a review of Kinberg's material. Clearly, Kinberg's name was published earlier than Quatrefages. The two names do not apply to the same species. The name *E. tentaculata* Quatrefages, while well known in the systematic literature, has not been used extensively in non-taxonomic contexts, thus there are no grounds for setting aside the rules of priority. Ehlers' name, *E. laticeps*, is the valid name for this species.

Eunice laticeps has been confused with a number of similar species; a detailed review of the problem is in preparation; the relation to similar species known from New Zealand and Australia is indicated in the key and table.

Eunice leuconuchalis Benham, 1900

Eunice leuconuchalis Benham, 1900: 21–22.

Remarks. Day & Hutchings (1979: 115) indicated that the type of *E. leuconuchalis* might be present in the Otago Museum, New Zealand. An inquiry showed that



Figs 46–50. *Eunice laticeps* Ehlers, 1868. 46, anterior end, lateral view; 47, parapodium 50, anterior view; 48, pectinate seta, parapodium 50; 49, compound falciger, parapodium 50; 50, subacicular hook, parapodium 50. (Holotype of *Eunice tentaculata* Quatrefages, 1866, MNHN, Paris, A1(R.)-1868-No. 52b.)

no material of this species is present in the holdings of that Museum (A.C. Harris, in litt.).

Benham's description includes the following statements: *Eunice leuconuchalis* is very common. The antennae are moniliform and the median antenna reaches setiger 4 and is the longest of the antennae. Branchiae are present from setiger 7 through setiger 35 and have up to 15 filaments.

The maxillary formula was in part indicated by Benham (1900) as 1 + 1, 5 + ?, 6 + 0. The species was considered synonymous with *E. australis* by Ehlers (1907: 12) and listed as such without comment by Fauvel (1917: 228). The differences between *E. leuconuchalis* as described by Benham and *E. australis* as described above based on the type specimen are minor and *E. leuconuchalis* is here considered a synonym of *E. australis* as originally suggested by Ehlers (1907).

Eunice plicata Baird, 1869

Figs 51–55

Eunice plicata Baird, 1869: 348–349.

Material examined. HOLOTYPE: BM(NH) ZH 1861.9.20.25; Fremantle, Australia, coll. Bowerbank.

Description. Holotype complete, but in 2 pieces; 126 setigers; 80 mm long; 5 mm wide at the widest; length through setiger 10, 8 mm.

Prostomium (Fig. 51) 2 short, rounded lobes, distinctly narrower than peristomium. Antennae very thick, prominent, digitiform. Outer lateral antennae reaching posterior edge of first peristomial ring; inner lateral and median antennae reaching setiger 2, with short basal ceratophores and 2 or 3 long articulations. Peristomium ventrally widely flaring; nuchal fold very deep; separation between rings distinct dorsally only; anterior ring about 9 times longer than posterior ring. Peristomial cirri without articulations; reaching middle of peristomium.

Maxillary formula 1 + 1, 4 + 4, 6 + 0, 6 + 7 and 1 + 1. Mx III part of distal arc with left Mx IV and V.

Branchiae (Fig. 52) setiger 7 to 115, all pectinate except last 30 pairs; maximum 5 filaments; filaments short; thick. Branchial stems very short; branchiae appearing nearly palmately branching. Filaments shorter than notopodial cirri in all but a few median segments.

Parapodia ventrolateral in first setigers, strictly lateral from setiger 10. Acicular lobes (Fig. 52) short, triangular. Presetal lobes low folds. Postsetal lobes as long as setal lobes in anterior setigers, reduced to low folds by setiger 30. Ventral cirri anteriorly thick, tapering, projecting as far as postsetal lobes, strongly inflated in median setigers; distal tip lost by setiger 50; ventral cirri present only as inflated glandular ridges along ventral side of neuropodia. Notopodial cirri thick, basally somewhat inflated, with 2 or 3 distinct articulations. Limbate setae slender, a few in all parapodia. Pectinate setae (Fig. 53) flat, flaring, with about 15 teeth; 1 marginal tooth slightly longer than

other. Shafts of compound hooks (Fig. 54) tapering, marginally smooth; appendages bidentate; distal teeth smaller than proximal teeth and curved at right angle. Hoods bluntly rounded. Notopodial aciculae black. Neuropodial aciculae black, straight, tapering, distally bluntly pointed, up to 3 in a parapodium. Subacicular hooks (Fig. 55) from setiger 25, black, bidentate; both teeth pointing distally and similar in size.

Remarks. As far as known, this species has remained unreported since it was briefly described by Baird (1869); it belongs to group B2 (Fauchald, 1970). Relations between *E. plicata* and other taxa from New Zealand and Australia are indicated in the Key and Table 1.

Nothing is known of its habitat, beyond what is indicated above.

Eunice pycnobranchiata McIntosh, 1885

Figs 56–61

Eunice pycnobranchiata McIntosh, 1885: 249–297, pl. 39, figs 13–15, pl. 21A, figs 4–5, textfigs 54–55.

Material examined. SYNTYPE: BM(NH) ZK 1921.5.1.1997; *Challenger* stn 162, off East Moncoeur Island, Bass Strait, 39°10'30"S, 146°37'E, 38–40 fms, dredged, sand, 2 April 1874. SYNTYPE: BM(NH) ZK 1921.5.1.1998; *Challenger* stn 163A off Port Jackson, 20–25 fms, rock.

Description. Port Jackson syntype incomplete; 63 segments; 50 mm long, 8 mm wide; length through setiger 10, 12 mm. Bass Strait syntype; 76 setigers; 55 mm long; 10 mm wide; length through setiger 10, 10 mm.

Port Jackson syntype frontally dissected; jaws now missing. Prostomium (Fig. 59) frontally rounded; covered by nuchal fold. Antennae reaching second peristomial ring. Outer lateral antennae somewhat shorter than other antennae; irregularly, but distinctly articulated with up to 15 articulations. Peristomium flaring anteriorly; separation between peristomial rings distinct dorsally and ventrally; anterior ring $\frac{5}{8}$ of peristomial length. Peristomial cirri not reaching front edge of peristomium, with three articulations.

Maxillary formula (rewritten from McIntosh, 1885, textfigure 54) 1 + 1, 5 + 5, 6 + 0, 6 + 8, 1 + 1. Mx III part of distal arc with left Mx IV and V.

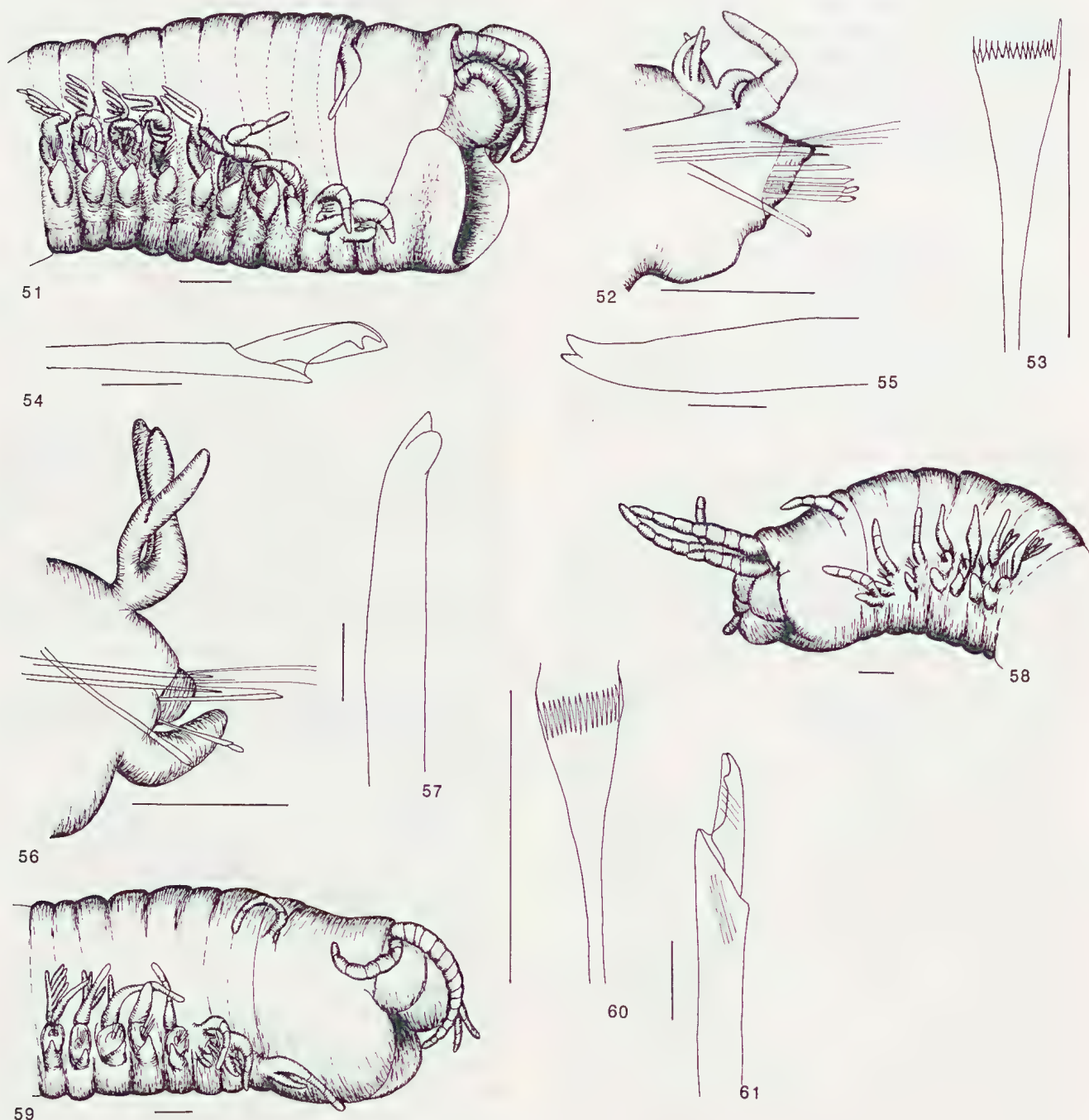
Branchiae (Fig. 56) from setiger 6 to end of both fragments. Maximum 4 short, thick filaments.

Acicular lobes (Fig. 56) rounded in all setigers. Presetal lobes low, transverse folds. Anterior postsetal lobes forming collars around dorsal edge of acicular lobes; posterior postsetal lobes low transverse folds. Ventral cirri digitiform; prominent in all setigers; basal inflated region indistinct. Anterior notopodial cirri digitiform with 2–4 irregular articulations; becoming basally somewhat inflated and loose articulations in branchial region. Limbate setae slender. Pectinate setae (Fig. 60) flat, flaring, with about 15 teeth; both marginal teeth slightly longer than other teeth. Shafts of compound hooks (Fig. 61) tapering, smooth, with

internal striations; appendages short, bidentate; proximal teeth short, triangular; distal teeth long, nearly erect. Aciculae black, tapering, paired in all but the first few setigers. Subacicular hooks (Fig. 57) from setiger 28 or 29; black, bidentate; distal teeth much smaller than proximal teeth; both teeth pointing obliquely distally.

Remarks. The Port Jackson syntype was described in detail by McIntosh and most of the description and

illustrations above are based on this specimen. The specimen from Bass Strait differs slightly from the specimen from Port Jackson in the length of the antennae (Fig. 58) and in the development of the branchiae, which tend to be more prominent in the Bass Strait specimen than in the other specimen. These differences are not considered to be of value as specific characters. McIntosh apparently got the information for Station 163A confused. The information given here is



Figs 51–61. *Eunice plicata* Baird, 1869. 51, anterior end, lateral view; 52, parapodium 46, anterior view; 53, pectinate seta, parapodium 46; 54, compound falciger, parapodium 46; 55, subacicular hook, anterior 46. (Holotype, BM(NH) ZH 1861.9.20.25). *Eunice pycnbranchiata* McIntosh, 1885. 56, parapodium 32, anterior view; 57, subacicular hook, parapodium 32; 58, anterior end, lateral view; 59, anterior end, lateral view; 60, pectinate seta, parapodium 32; 61, compound falciger, parapodium 32. (58 from Syntype, BM(NH) 1921.5.1.1997, all other figures of Syntype, BM(NH) ZK 1921.5.1.1998.)

taken from the official published station list for the expedition.

Eunice pycnobranchiata has been considered a junior synonym of *E. afra* and *E. laticeps*. *Eunice afra* has branchiae from about setiger 18 and *E. pycnobranchiata* has branchiae from setiger 6. *Eunice laticeps* has distinctly inflated ventral cirri in a median region and up to 18 branchial filaments; *E. pycnobranchiata* has digitiform ventral cirri in all setigers and up to 6 branchial filaments.

Eunice quoya Quatrefages, 1866

Eunice quoya Quatrefages, 1866: 318.

Remarks. No material of this species is available in MNHN (J. Renaud-Mornant, in litt.). The following translation of Quatrefages text indicates what is known about the species:

1. Diagnosis (in Latin, translation with terminology updated): "Prostomium deeply bilobed. Antennae lightly articulated. Peristomium long. Superior maxillae robust, the inferior ones with 4–5 teeth. Maxilla III (?) with two teeth. Mandible with entire margin. Notopodial cirri rather long, ventral cirrus thick, fused to the acicular lobe. Branchiae with 7–8 branchial filaments."

2. Comments (in French, translation with updated terminology): "This species is very close to the preceding one (*Eunice tentaculata* = *E. laticeps* is the species to which the comment refers, K. Fauchald comm.), even if the single specimen reported by Quoy & Gaimard is of considerably smaller dimensions. The prostomium, as in *E. tentaculata*, is large and deeply bilobed. But the antennae are indistinctly articulated and do not appear moniliform. The peristomium is equal in length to the next four segments, but the fold that carries the peristomial cirri resembles even more than in the preceding species a true segment and is equal in length to the first body segment. The peristomial cirri are nearly smooth. The upper jaws are robust as are the inferior ones, the latter carry 4–5 teeth which are proportionally smaller than in the preceding species. One finds only a single denticle on each side (this comment may refer to maxilla IV, K. Fauchald). The mandible is fused and is only shallowly incised along the anterior margin. The body is rounded in cross-section, rather than depressed, but this difference may be a result of age, as I have been able to demonstrate for *Marphysa sanguinea*. The parapodia are very inconspicuous. The notopodial cirri are shorter than in the preceding species. The ventral cirrus is thick, elongated and emerges directly at the base of the neuropodium; the latter is poorly developed. The setae resemble that of the preceding species, but the appendage is better developed than in that species. The branchiae do not start until towards setiger 20, and do not have more than 7–8 relatively short filaments."

Quatrefages thus essentially gave a differential

diagnosis of the species with respect to *Eunice laticeps*. It is not clear from his description if the species has dark (black) acicula and subacicular hooks. Assuming that such are present, the species should be compared to *E. afra* rather than to *E. laticeps* on the basis of the distribution of branchiae. The type locality is given as "Nouvelle-Hollande", which takes in the whole continent. Without access to the types, the species is indeterminate.

Eunice rubella Knox, 1951

Figs 62–66

Eunice rubella Knox, 1951: 66–69, figs 6–12.

Material examined. HOLOTYPE: CM; Banks Peninsula, New Zealand, 80 fms.

Description. Holotype 2 fragments; anterior fragment 46 segments; 27 mm long; 2 mm wide; length through setiger 10, 8 mm. Posterior fragment including pygidium 48 setigers; 21 mm long.

Prostomium (Fig. 62) short, truncate, anteriorly shallowly split; nuchal fold everted. Antennae reaching middle of peristomium, relatively stout; all antennae very distinctly articulated with moniliform articulations; maximum number of articulations 7 in inner lateral antennae; innermost article $\frac{1}{2}$ of each antenna. Black eyes between bases of outer and inner lateral antennae. Peristomium cylindrical, more than twice as long as prostomium; separation between peristomial rings distinct dorsally and laterally, but indistinct ventrally; anterior ring $\frac{3}{4}$ of peristomial length. Peristomial cirri reaching about middle of peristomium; with 3 articulations.

Jaw apparatus dissected out; now missing. Maxillary formula (Knox, 1951, fig. 12) 1 + 1, 5 + 6, 6 + 0, 6 + 7 and 1 + 1. Mx III short; part of distal arc with left Mx IV and V.

Branchiae (Fig. 63) from setiger 5; maximum of 2 short, thick filaments between setigers 7 and 29; otherwise all branchiae single filaments. Branchiae originally described as present to setiger 80; distribution on 2 fragments present agreeing with this pattern.

Anterior parapodia very short; acicular lobes distally truncate. Pre- and postsetal lobes low folds. Anterior ventral cirri thickset, tapering, becoming distinctly ventrally inflated with triangular tips by setiger 8; inflated region reduced by setiger 27; further posteriorly, ventral cirri forming large, open scoops (Fig. 63) covering emergent part of subacicular hooks. Anterior notopodial cirri thick, pyriform, with 3 articulations, becoming digitiform and losing articulations by setiger 20. Limbate setae slender. Pectinate setae (Fig. 65) tapering, flat, with 12 teeth; both marginal teeth slightly longer than other teeth. Shafts of compound hooks (Fig. 66) tapering; cutting edge finely dentate; appendages short, rather wide, bidentate; teeth short, blunt, roughly of same size. Hoods distally bluntly truncate, marginally serrated. Aciculae black, very thick, tapering to slender

tips, bent towards dorsal side, paired in median and posterior parapodia. Subacicular hooks (Fig. 64) from setiger 28, black, bidentate, distinctly curved; proximal teeth large, triangular; distal teeth short, erect, thick.

Remarks. The holotype was originally described as being in three pieces including 112 segments measuring 60 mm; presumably a fragment of 16 segments, 12 mm long, is now missing.

Eunice rubella differs sharply from other species with black, bidentate subacicular hooks from the region by having very strongly beaded antennae and by the poor development of the branchiae.

Eunice torresiensis McIntosh, 1885

Figs 67–70

Eunice torresiensis McIntosh, 1885: 270–272, pl. 37, figs 18–21, pl. 19A, figs 12–13, textfigs 32–33 (in part).

Material examined. LECTOTYPE and PARALECTOTYPE: BM(NH) ZK 1885.1.12.193; *Challenger* stn 186, Torres Strait, 10°30'S, 142°18'E, 8 fms, coral sand.

Description. Lectotype complete mature female with large eggs, cut in 2 pieces; 72 setigers; 47 mm long; 3 mm wide; length through setiger 10, 6.5 mm. Other specimen, illustrated by McIntosh; 16 setigers; cut, presumably from a much longer specimen.

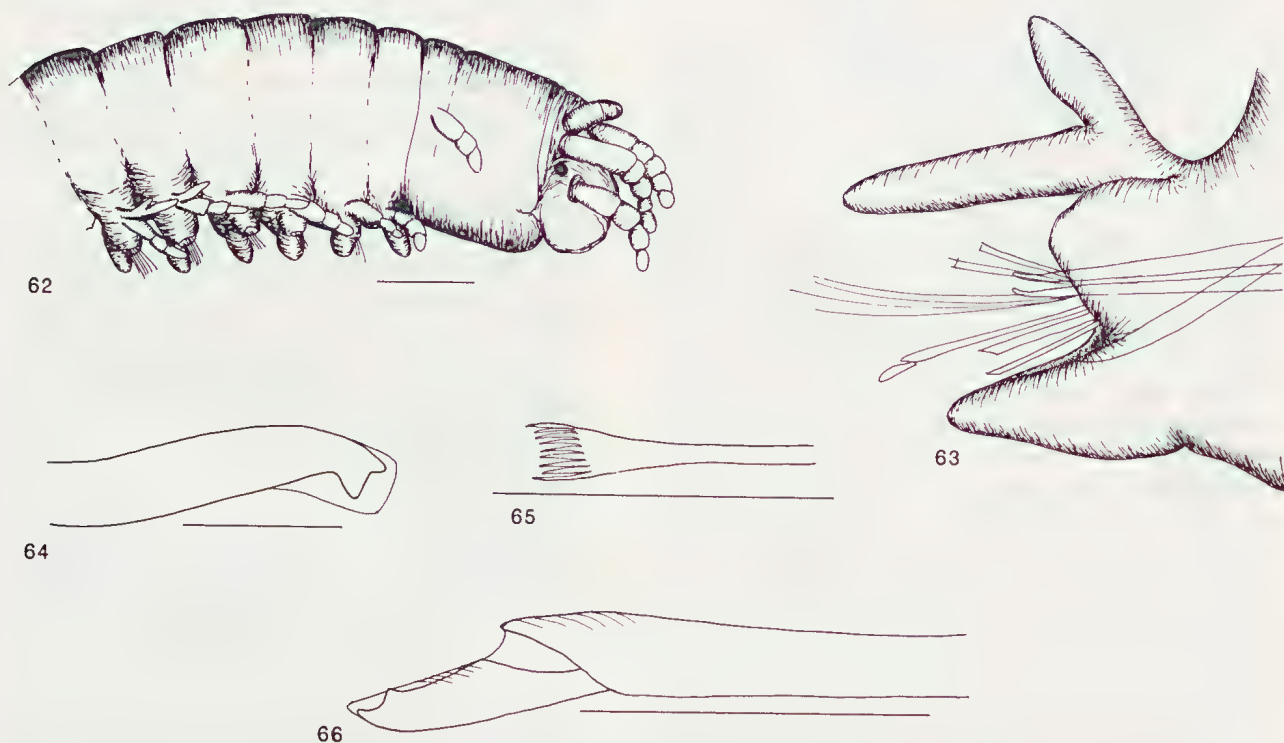
Prostomium (Fig. 67) 2 rounded lobes, well separated medially; about $\frac{1}{3}$ narrower than peristomium. Antennae strongly articulated; distal articulations

moniliform; maximal number of articulations about 30 in median antenna. Outer lateral antennae reaching setiger 1; inner lateral antennae reaching setiger 7; median antenna reaching setiger 9. Reddish eyes between bases of outer and inner lateral antennae. Peristomium about as wide as anterior part of body; separation between peristomial rings indistinct, noticeable only ventrally and in front of cirral bases; anterior ring nearly $\frac{3}{4}$ of peristomial length. Peristomial cirri slender, reaching front edge of peristomium, with about 12 articulations.

Jaws dissected out on paralectotype; maxillary formula (rewritten from McIntosh, 1885: 271, fig. 32) 1 + 1, 4 + 3, 6 + 0, 5–6 + 8, 1 + 1. Mx III long; located behind left Mx II.

Branchiae (Fig. 68) from setiger 5 as single filaments; number of filaments increasing to maximum of 7 by setiger 15, thereafter decreasing rapidly to 3; this number maintained in middle region of the body; towards posterior end number of filaments again increasing to 7; this number maintained in all but last few segments.

Acicular lobes (Fig. 68) distally truncate. Pre- and postsetal lobes low, transverse folds. Ventral cirri digitiform in prebranchial region, becoming basally inflated, retaining distinct tips in middle region; inflated region reduced by setiger 30; ventral cirri again digitiform in posterior setigers. Notopodial cirri long, digitiform in all setigers, with up to 6 moniliform articulations in prebranchial segments; articulations becoming elongated and reduced in number to 4 in



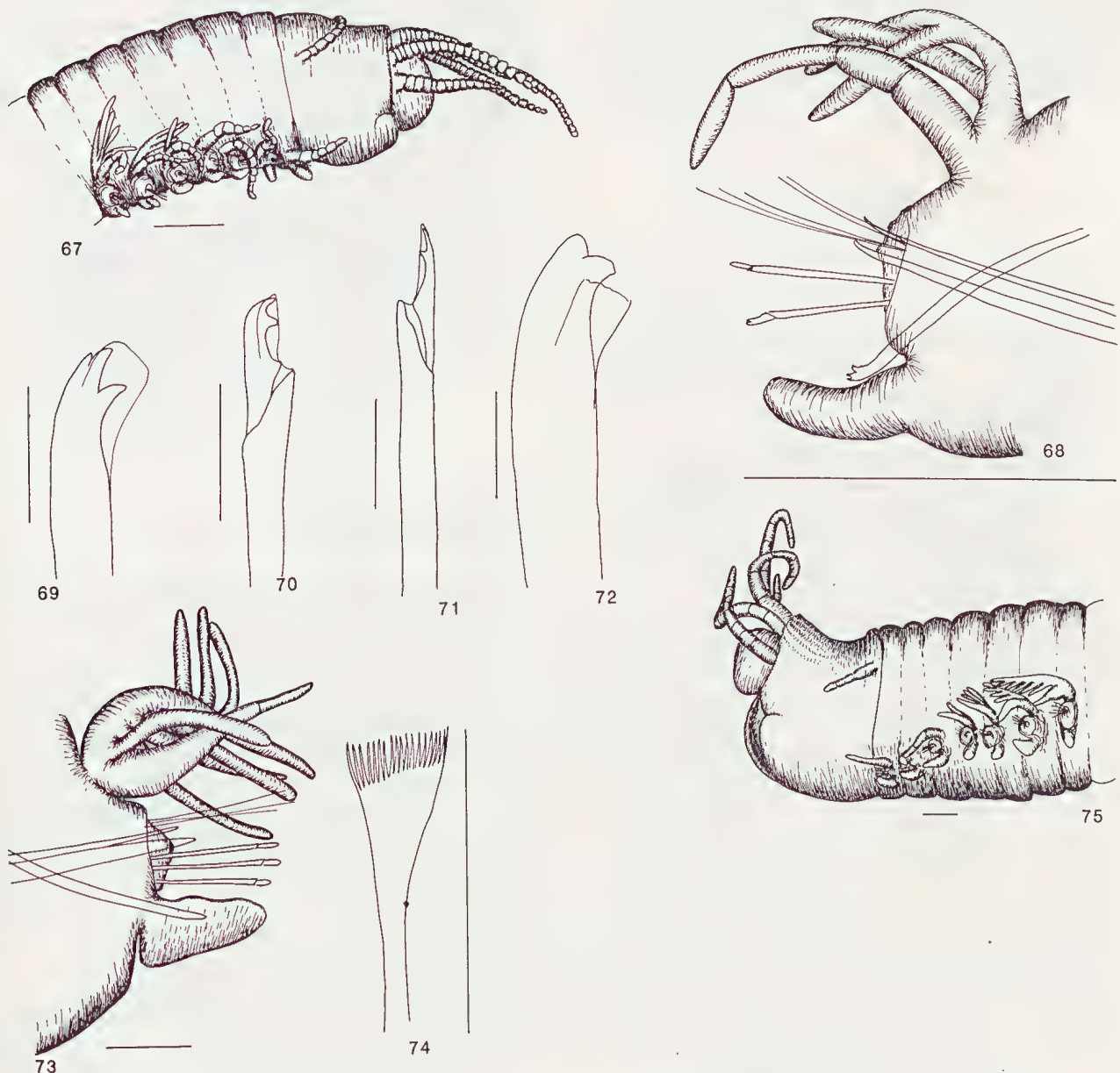
Figs 62–66. *Eunice rubella* Knox, 1951. 62, anterior end, lateral view; 63, parapodium 45, anterior view; 64, subacicular hook, parapodium 45; 65, pectinate seta, parapodium 45; 66, compound falciger, parapodium 45. (Holotype, CM).

branchial region. Shafts of compound hooks (Fig. 70) smoothly tapering, without ornamentation; appendages short, distally sharply bent, bidentate; both teeth large. Hoods bluntly rounded. Aciculae yellow, paired, tapering to sharp tips, bent. Subacicular hooks (Fig. 69) from setiger 24, yellow, tridentate, with large main fangs and 2 smaller distal teeth in crests.

Remarks. The type material of *E. torresiensis* originally consisted of two large anterior ends, one small complete specimen currently in two pieces and one small anterior end. One of the large fragments and the small fragment have both been dissected. The small fragment

is the specimen illustrated by McIntosh (1885: pl. 38, fig. 18). The two large anterior fragments do not belong to the same species as the small specimens. The large fragments have black, bidentate subacicular hooks, the small specimens have yellow, tridentate subacicular hooks, among other differences. The small specimens were described in great detail by McIntosh; the other two specimens belong to *E. tribranchiata* described by McIntosh from the same station (see below) on the basis of a posterior fragment only.

Eunice torresiensis resembles *E. antennata* in having moniliform articulations on the antennae and tridentate, yellow subacicular hooks. It further resembles *E.*



Figs 67–75. *Eunice torresiensis* McIntosh, 1885. 67, anterior end, lateral view; 68, parapodium 34, anterior view; 69, subacicular hook, parapodium 34; 70, compound falciger, parapodium 34. (Syntype, BM(NH) ZK 1885.12.1.193.) *Eunice tribranchiata* McIntosh, 1885. 71, compound falciger, parapodium 35; 72, subacicular hook, parapodium 35; 73, parapodium 35, anterior view; 74, pectinate seta, parapodium 35; 75, anterior end, lateral view. (Syntype of *Eunice torresiensis*, ZK 1885.12.1.193.)

antennata in having a median region of the body with reduced number of branchial filaments. *Eunice torresiensis* differs from *E. antennata* in the shape of the aciculae, which are bent and tapered in the former and hammer-headed in the latter. *Eunice torresiensis* has bidentate compound falcigers, *E. antennata* has tridentate falcigers.

Eunice torresiensis resembles *E. elseyi* in the shape of the prostomium, the antennae and the aciculae, but differs from it in that the branchiae have a reduced number of filaments in a median region in the former, but not in the latter and in that the overall maximal number of branchial filaments is about twice as high in the latter as in the former.

Eunice torresiensis resembles *E. bassensis* in having tridentate yellow subacicular hooks; the two species can be separated on the distribution of branchial filaments and the presence of white epidermal granules in the latter, but not in the former.

Eunice tribranchiata McIntosh, 1885

Figs 71–75

Eunice tribranchiata McIntosh, 1885: 297, pl. 21A, figs 6–7. *Eunice torresiensis* McIntosh, 1885: 270–272, pl. 37, figs 18–21, pl. 19A, figs 12–13, textfigs 32–33 (in part).

Material examined. HOLOTYPE: BM(NH) ZK.1885.12.1.205; 2 SYNTYPES of *Eunice torresiensis*, BM(NH) ZK.1885.12.1.193; *Challenger* stn 186, Torres Strait, 10°30'S, 142°18'E, 8 fms, coral sand.

Description. Holotype posterior fragment of 90 setigers. Specimen described and illustrated (see comment below) incomplete; 35 setigers; 31 mm long; 7 mm wide; length through setiger 10, 13 mm. Other specimen incomplete; 18 setigers; 15 mm long; 8 mm wide; length through setiger 10, 11 mm.

Prostomium (Fig. 75) 2 well separated, rounded halves, distinctly narrower than peristomium. Antennae with maximum 6 articulations; most articulations longer than wide. Outer lateral antennae reaching second peristomial ring; inner lateral and median antennae reaching setiger 1. Peristomium as wide as anterior part of body; separation between peristomial rings well marked dorsally, less well marked ventrally, indistinct laterally; anterior ring more than $\frac{1}{2}$ of peristomial length. Peristomial cirri slightly inflated basally, reaching middle of peristomium, with 5 articulations.

Maxillary formula (illustrated in McIntosh, 1885, plate 37, fig. 20) 1 + 1, 4 + 4, ? + 0, 6 + 6, 1 + 1; unpaired maxilla III absent in illustration, possibly reduced and closely appressed to left Max IV.

Branchiae (Fig. 73) from setiger 4 or 5, continuing to ends of fragments; all branchiae consisting of 2 or more filaments; maximum 8 filaments.

Acicular lobes (Fig. 73) distally triangular, with both aciculae emerging at tip. Pre- and postsetal lobes low transverse folds in all setigers. Anterior ventral cirri very large, digitiform, becoming scoop-shaped with

subacicular hooks resting in base of scoop further posteriorly. All notopodial cirri basally inflated, with 2 or 3 long, indistinct articulations. Limbate setae slender, marginally serrated. Pectinate setae (Fig. 74) flat, flaring, with about 20 teeth; all teeth of about same length. Shafts of compound hooks (Fig. 71) long, essentially untapered, marginally smooth; appendages narrow, bidentate; proximal teeth larger than distal teeth; distal teeth very nearly erect, tapering to pointed tips. Hoods short, bluntly pointed. Aciculae dark, distally tapering, straight. Subacicular hooks (Fig. 72) from setiger 30, black, single, bidentate; both teeth similar; hoods short, truncate.

Remarks. The holotype of *E. tribranchiata* is a posterior fragment consisting of 90 median and posterior setigers. Two of the four syntypes of *Eunice torresiensis* described from the same station agree with this posterior fragment in all important features. The description is based on these two anterior ends.

Eunice tribranchiata resembles *E. laticeps* closely in that it has black, bidentate subacicular hooks, pectinate branchiae present from one of the first setigers and the distribution of the subacicular hooks also appears to fit. It differs from *E. laticeps* in the shape of the compound hooks and the subacicular hooks and in the structure of the pectinate setae. In addition, the scooped ventral cirri are characteristic of *E. tribranchiata*; all ventral cirri are tapering or basally inflated in *E. laticeps*.

Eunice tridentata Ehlers, 1905

Figs 76–82

Eunice tridentata Ehlers, 1905: 288–290, pl. 9, figs 3–10.

Material examined. HOLOTYPE: ZMH PE 699, New Zealand.

Description. Holotype complete mature female with eggs; 185 setigers; 170 mm long; 7 mm long; length through setiger 10, 12 mm.

Prostomium (Fig. 76) 2 very short, rounded lobes, well separated medially, less than $\frac{1}{2}$ as long as peristomium. Antennae slender, articulated; maximum 8 cylindrical articulations in median antenna. Outer lateral antennae reaching posterior margin of peristomium; inner lateral antennae reaching setiger 2; median antenna reaching posterior edge of setiger 3. Peristomium forming thick collar around prostomium; separation of peristomial rings very distinct dorsally and ventrally, appearing nearly as separate segment, but indistinct laterally; anterior ring $\frac{1}{2}$ of peristomial length. Peristomial cirri slender, reaching nearly tip of the prostomium, without articulations.

Jaw apparatus currently missing. Maxillary formula (Ehlers, 1905: pl. 9, fig. 4) 1 + 1, 7 + 6, ?14 + 0, 7 + 10 and 1 + 1. Mx III long, located behind left MX II.

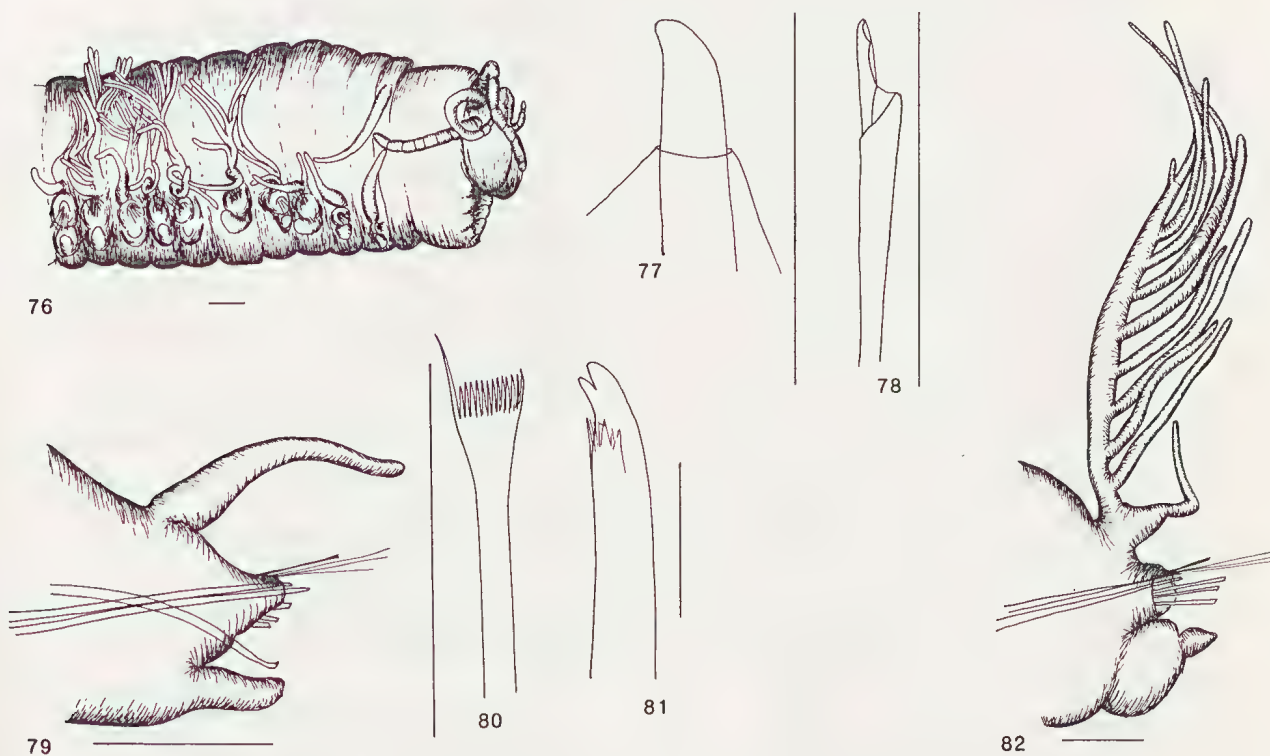
Branchiae (Fig. 82) from setiger 3 through 80; first and last 15 pairs simple filaments; other branchiae pectinate with soft, pliable branchial stems and long, slender branchial filaments; maximally 14 branchial

filaments at setiger 30.

Anterior acicular lobes rounded, with aciculae situated above highest point of lobe; posterior acicular lobes (Figs 79, 82) triangular, nearly pointed, with aciculae emerging at tips. Anterior presetal lobes obliquely transverse, sloping from high points at dorsal margin towards base of acicular lobe at ventral margin; posterior presetal and all postsetal lobes transverse low folds. First 4 ventral cirri thick, sharply tapering, becoming strongly basally inflated in next 20 parapodia, retaining distinct, nearly triangular tips; postbranchial ventral cirri becoming increasingly digitiform, gradually losing basal inflation. Prebranchial notopodial cirri pyriform, about $\frac{1}{2}$ as long as peristomial cirri, becoming distinctly inflated basally, abruptly tapering with long digitiform tips in branchial region; postbranchial notopodial cirri pyriform, shorter than those in prebranchial region. Limbate setae slender, nearly capillary. Pectinate setae (Fig. 80) flat, flaring, with about 15 teeth; 1 marginal tooth prolonged. Shafts

of compound hooks (Fig. 78) thick, smoothly tapering, without marginal dentition; appendages very small, narrow, bidentate; proximal teeth triangular; distal teeth nearly erect, much smaller than proximal teeth. Hoods short, blunt. Aciculae yellow, paired (Fig. 77), distally bent towards ventral side. Subacicular hooks (Fig. 81) from setiger 51, irregularly missing in several setigers, yellow, bidentate, distally abruptly tapered; teeth similar in size, both directed obliquely distally.

Remarks. Records of *E. tridentata* from the northern hemisphere must be considered doubtful. The species has been confused with a series of rather similar species, all with branchiae starting on setiger 3 and limited to a few anterior segments. Fauchald (1969) reviewed a series of related species, but did not consider *E. tridentata*. A complete revision of the genus will clarify the relation between this species and similar species from parts of the world.



Figs 76–82. *Eunice tridentata* Ehlers, 1905. 76, anterior end, lateral view; 77, acicula, parapodium 20; 78, compound falciger, parapodium 20; 79, parapodium 162, anterior view; 80, pectinate seta, parapodium 162; 81, subacicular hook, parapodium 162; 82, parapodium 20, anterior view. (Holotype, ZMH PE 699.)

KEY TO THE SPECIES OF *EUNICE* REPORTED FROM AUSTRALIA AND NEW ZEALAND

Included in the key are all species listed by Day & Hutchings (1979) not originally described from Australia and New Zealand, in addition to the species reviewed here. The key must be considered temporary pending review of the types of species described from areas outside the region considered in this paper. I assumed that the original descriptions of all these species (as revised where appropriate) are accurate and that the material from Australia and New Zealand conform to these descriptions. Both assumptions are of dubious validity. The key has value in that it will allow workers on Australian material to assess whether they in fact have the species covered, as originally described, in their collections, or if they have new taxa or species not yet reported from the region.

The species treated in this review are marked by an asterisk.

1. Subacicular hooks and aciculae yellow or clear. 2
- Subacicular hooks and aciculae brown or black. 12
2. Subacicular hooks distally bidentate. 3
- Subacicular hooks distally tridentate. 4
3. Anterior parapodia with compound spinigers; compound falcigers present
in median and posterior setigers. *tubifex*
- Anterior parapodia without compound spinigers; compound falcigers present
in all setigers. **tridentata*
4. Branchiae present only on the anterior $\frac{1}{2}$ – $\frac{2}{3}$ of the body. 5
- Branchiae present to the posterior end. 7
5. Compound falcigers with distally blunt or rounded hoods. **australis*
- Compound falcigers with mucronate or sharply pointed hoods. 6
6. Antennae without articulations. *indica*
- Antennae articulated. *vittata*
7. Every branchia consisting of a single filament. *makemoana*
- At least some branchiae branched. 8
8. Anterior and far posterior branchiae with higher number of filaments than
median ones. 9
- Numbers of branchial filaments decreasing from a peak number at or near
setiger 20, or most branchiae with similar numbers of filaments. 10
9. Aciculae distally pointed and bent. **torresiensis*
- Aciculae distally hammer-headed. *antennata*
10. Integument with white pigment patches; maximum number of branchial
filaments about 10. **bassensis*
- Integument without white pigment patches; maximum number of branchial
filaments more than 15. 11
11. One acicula flattened with a rounded head, the other one bidentate;
subacicular hooks with all 3 teeth in the same plane. **aequabilis*
- Both aciculae distally bidentate; subacicular hooks with the distal tooth lateral
to the other teeth. **elseyi*
12. Branchiae absent. 13
- Branchiae present. 14

13. Antennae without articulations. *gracilis*
 —Antennae beaded. **curticirris*
14. Branchiae first present anteriorly to setiger 10. 15
 —Branchiae first present posteriorly to setiger 10. 25
15. Branchiae limited to the anterior $\frac{1}{2}$ of the body. **rubella*
 —Branchiae present through most of the posterior part of the body. 16
16. Ventral cirri distinctly inflated basally in median setigers. 17
 —Ventral cirri tapering in all setigers. **pynobbranchiata*
17. Inflated ventral cirri with free distal tip in all setigers. 18
 —Inflated ventral cirri without free tip in median and posterior setigers. **plicata*
18. Ventral cirri in median and posterior setigers forming a scoop around the
 lower edge of the parapodia. **tribranchiata*
 —Ventral cirri not wrapped around the lower edge of the parapodia in any
 setigers. 19
19. Antennae with monoliform articulations. 20
 —Antennae with long articulations. 21
20. Branchiae first present from setiger 3, with maximally 8 filaments. *grubei*
 —Branchiae first present from setiger 5, with maximally 15 filaments. **bowerbanki*
21. Branchiae with a very long stem and many (25+) very short branchial
 filaments. **franklini*
 —Branchial stem short, or if branchial stem long, then filaments not unusually
 short. 22
22. Branchiae first present from setigers 3–4. 23
 —Branchiae first present from setigers 6–8. *aphroditois*
23. Maximally 18 branchial filaments. **laticeps*
 —Maximally 6–8 branchial filaments. 24
24. Last 20–30 pairs of branchiae single filaments, peristomial cirri not reaching
 front of peristomium. *longicirris*
 —Last 20–30 pairs of branchiae with 3 filaments, peristomial cirri reaching well
 beyond front of peristomium. *microprion*
25. Aciculae hammer-headed. *filamentosa*
 —Aciculae tapering, straight or bent. 26
26. Branchiae first present from setiger 19, subacicular hooks from setiger 28. 27
 —Branchiae first present from setigers 18–21, subacicular hooks from setigers
 35–42. 28
27. Body strongly flattened with crowded segments from about setiger 20. **dilatata*
 —Body at most lightly flattened in median and posterior setigers; segments not
 crowded. *complanata*
28. Maximum number of branchial filaments 4–6. *afra afra*
 —Maximum number of branchial filaments 4 or less. *afra paupera*

ACKNOWLEDGEMENTS. I would like to thank the Director of the Australian Museum, Dr Desmond Griffin and my host in Sydney Dr Pat Hutchings for their hospitality during my stay in 1983. I would also like to thank the curators of the following institutions for loan of material: Museum Przdonicze, Wroclaw (MPW), Poland; Muséum National d'Histoire Naturelle (MNHN), Paris; British Museum (Natural History) (BM[NH]), London and Zoologisches Institut und Staatsmuseum, Hamburg (ZMH). Drs Meredith L. Jones and Pat Hutchings critically reviewed the manuscript.

References.

- Baird, W., 1869. Remarks on several genera of Annelides belonging to the group Eunicea, with a notice of such species as are contained in the collection of the British Museum and a description of some others hitherto undescribed. *Journal of the Linnean Society of London, Zoology* 10: 341-361.
- Benham, W.B., 1900. Polychaeta. In 'Report on experimental trawling' (ed. L.F. Ayson). *Journal of the House of Representatives of New Zealand* 1900, appendix H15A: 1-24.
- [Claparède, E.], 1865. Review of: Quatrefages, A. de. Note sur la classification des Annélides. (Comptes Rendus des Séances de l'Académie des Sciences, Paris, 27 mars 1865). *Bibliothèque Universelle et Revue Suisse - Archives des Sciences Physiques et Naturelles*, Genève, séries 2, 22: 346-355.
- Day, J.H. & P.A. Hutchings, 1979. An annotated check-list of Australian and New Zealand Polychaeta, Archiannelida and Myzostomida. *Records of the Australian Museum* 32(2): 80-161.
- Ehlers, E. 1868. Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt. Second section: 269-748. Wilhelm Engelmann, Leipzig.
- 1905. Anneliden den Sammlung Schauinsland. *Ergebnisse einer Reise nach dem Pazific, Schauinsland, 1896-97. Zoologische Jahrbücher*, Jena, Abteilung für Systematik 22: 281-302.
- 1907. Neuseeländische Anneliden. II. *Abhandlungen der königlichen Gesellschaft der Wissenschaften zu Göttingen. Mathematisch-Physikalische Klasse. Neue Folge* 5(4): 1-31.
- Fauchald, K., 1969. A revision of six species of the *flavus-bidentatus* group of *Eunice* (Eunicidae: Polychaeta). *Smithsonian Contributions to Zoology* 6: 1-15.
- 1970. Polychaetous annelids of the families Eunicidae, Lumbrineridae, Iphitimidae, Arbellidae, Lysaretidae and Dorvilleidae from western Mexico. *Allen Hancock Monographs in Marine Biology* 5: 1-335.
- Fauvel, P. 1917. Annélides polychètes de l'Australie meridionale. *Archives de zoologie expérimentale et générale* 56:159-277.
- Grube, A.-E., 1877. [Die von der *Gazelle* mitgebrachten Anneliden, zu denen noch zwei von Dr Buchholz gesammelte kommen]. *Monatsberichte der deutsche Akademie der Wissenschaften zu Berlin* 1877: 509-554.
- 1878. [Familie Eunicea]. *Jahresbericht der Schlesische Gesellschaft für vaterlandische Cultur*, Breslau 55: 79-104.
- Hartman, O., 1948. The marine annelids erected by Kinberg with notes on some other types in the Swedish State Museum. *Arkiv för Zoologi*, Stockholm 42(1): 1-137.
- 1959, 1965. Catalogue of the polychaetous annelids of the world. *Allan Hancock Foundation Publications Occasional Paper* 23: 1-628 (1959). Supplement 1960-1965 and Index 23: 1-197 (1965).
- Knox, G.A., 1951. The polychaetous annelids of Banks' Peninsula. Part 2. A rock bottom fauna from 80 fathoms. *Records of the Canterbury Museum* 6(1): 61-81.
- 1960. Polychaeta Errantia. In: 'Biological Results of the Chatham Islands 1954 Expedition. Part 3.' *Bulletin of the New Zealand Department of Scientific and Industrial Research* 139(3): 77-143 (also issued as *Memoirs of the New Zealand Oceanographic Institute* 6: 77-146).
- McIntosh, W.C., 1885. Report on the Annelida Polychaeta collected by H.M.S. "Challenger" during the years 1873-76. *Challenger Reports* 12: 1-554.
- Monro, C.C.A., 1924. On the Polychaeta collected by H.M.S. "Alert", 1881-1882. Families Polynoidae, Sigalionidae and Eunicidae. *Journal of the Linnean Society, London Zoology* 36: 39-64.
- Quatrefages, A. de, 1865a. Note sur la classification des Annélides. *Comptes Rendu des Séances de l'Académie des Sciences*, Paris 40(13): 586-600.
- 1865b. Note sur la classification des annélides, et reponse aux observations de M. Claparède. *Annales des Sciences Naturelles*, Paris, series 5, 3: 253-296.
- 1866. *Histoire Naturelle des Anneles marins et d'eau douce. Annélides et Géphyriens*. Paris, Librairie Encyclopédique de Rôret 1: 1-588.
- Wright, E.P., 1866. Annelida. *Zoological Record* 1866: 578-600.

Accepted 10 July 1986.

Australian species of *Systemus* (Diptera: Dolichopodidae)

DANIEL J. BICKEL

Australian Museum,
P.O. Box A285, Sydney South, NSW 2000, Australia

ABSTRACT. *Systemus australis* and *S. curryi*, n. spp. are described from eastern Australia and Western Australia, respectively. *Systemus* is regarded as belonging to the dolichopodid subfamily Medeterinae.

BICKEL, DANIEL J., 1986. Australian species of *Systemus* (Diptera: Dolichopodidae). Records of the Australian Museum 38(5): 263–270.

Although adults of *Systemus* are rarely encountered in the field, more is known of the life history and immature stages of *Systemus* than any other dolichopodid genus. The majority of museum specimens are the results of rearings from tree-hole debris and sap-fluxes, supplemented by collections made using passive mass-sampling techniques, such as malaise and light traps. Apart from the two new Australian species treated below, 16 species previously have been described: nine palearctic, six nearctic and one neotropical (Steyskal, 1970; Vaillant, 1978). Of these, larval habitats are known for eight palearctic and four nearctic species, and the larval and pupal morphology of five species has been described in detail (also see Lundbeck, 1912; Wirth, 1952; and Krivosheina, 1973).

The larvae of all known species are characterised by a distinctive thumb-like ventral proleg on the first abdominal segment, readily differentiated from the creeping welts of the posterior segments. Larvae have been reared from moist tree-hole debris and bleeding ulcers associated with a number of north temperate hardwood species. Such microhabitats, especially tree-holes with rotting debris accumulated over a period of years, often support a rich invertebrate fauna, providing suitable prey for *Systemus* larvae. Vaillant (1978), in a review of subject, has termed this microhabitat a 'dendrotelme' biotope. Specimens of the new Australian species were all taken as adults in traps. However, suitable larval tree-hole habitats are commonly encountered in the Australian bush, especially in cavities formed on twisted, broken or partially burnt eucalyptus

trees. Rearings from eucalyptus cavity debris might determine the life history of Australian *Systemus*.

Materials and Methods

The abbreviations of repositories where specimens are housed are listed in the Acknowledgements. All measurements are in millimetres. Morphological terminology follows McAlpine (1981) and Bickel (1985). In describing the male hypopygium, the terms 'dorsal' and 'ventral' refer to morphological position prior to rotation and torsion. Thus, in figures showing a left lateral view of the hypopygium, morphologically dorsal is at the bottom while morphologically ventral is at the top.

TAXONOMY

Genus *Systemus* Loew

Systemus Loew, 1857: 34. Type species, *Rhaphium adpropinquans* Loew (des. Foote, Coulson & Robinson 1966: 517) = *pallipes* (Rosen).

Description. The following description of adult *Systemus* is based on examination of the new Australian species and males of two nearctic species, *S. shannoni* and *S. eucerus*, and on published descriptions and figures of the remaining species.

HEAD: eyes with tiny setulae between facets; fronto-clypeal suture complete; proboscis projecting anteriorly, keel-like, with 6 unsclerotized pseudotracheae; single

row of postorbitals present; scape without dorsal setae; 1st flagellomere with marked sexual dimorphism: in male lancet shaped, elongate, usually 2–3 times as long as basal width, bearing short apical arista; in female subovate, about as long as wide, bearing long apical arista; postcranium dorsally concave.

THORAX: mesoscutum distinctly flattened posteriorly; acrostichals biserial, posteriormost pair larger and laterally offset; 6 strong dorsocentrals; 1 postalar, 2 postsutural and 2 presutural supraalars, 2 notopleurals, 1 humeral, and 1 posthumeral present; lateral scutellars less than $\frac{1}{2}$ length of medians.

LEGS: coxa III with one strong lateral bristle; femora lacking anterior preapical bristles; only tibiae II and III with notable bristles, scattered dorsals and ventrals, with anterodorsal and posterodorsal pair at $\frac{1}{4}$; basitarsus III $< \frac{1}{2}$ length second tarsomere III.

WINGS: R_{4+5} and M subparallel but often bowed or flexed subapically; flexion present in distal sector of M, the 'bosse alaire'; $A_1 + Cu_A$ present.

ABDOMEN: lateral tergal margins of segments 2–5 in females only with 3–4 ovoid depressions, lacking in males.

MALE POSTABDOMEN: segment 7 forming an elongate peduncle, tergum and sternum 7 incompletely fused, separated by partially sclerotized pleural membrane (Fig. 3); hypopygial foramen left lateral; hypandrium fused to epandrium, immovable; 2 bristle-bearing epandrial lobes arising from inner wall of the genital chamber or fused to epandrium with only bristles remaining; surstylus usually bifurcate; cercus elongate, bristly.

FEMALE GENITALIA: fused terga 9+10 divided medially into 2 hemitergites, each bearing 4 spine-like acanthoporphores.

Key to Australian Species of *Systemus*

1. Femora II, III without anterior preapicals; scape dorsally bare; vertex not deeply excavated on either side of ocellar tubercle; posterior $\frac{1}{3}$ of mesoscutum distinctly flattened; vein M unbranched; male hypopygium on elongate peduncle formed by segment 7 or greatly enlarged; hypopygium exerted, never encapsulated or enfolded by preceeding abdominal segments. 2
 — Without above combination of characters. Various dolichopodid subfamilies
2. Arista apical; legs relatively short, length leg III $<$ twice wing length; hypopygium usually ovate; peduncle (segment 7) often elongated. 3
 — Arista dorsal; legs elongate, length leg III $>$ twice wing length; hypopygium usually globular, peduncle usually short. Neurigoninae
3. R_{4+5} and M subapically bowed; distal sector of M with flexion, the 'bosse alaire'; posterior pair acrostichals (ac) distinctly larger than preceeding pairs and offset laterally; 6 strong dorsocentrals (dc); antenna sexually dimorphic; male 1st flagellomere elongate, tapering, with short arista (Fig. 1); female 1st flagellomere subovate with long arista (Fig. 2); peduncle (abdominal segment 7) with tergum and sternum distinct (Fig. 3); female terga 9+10 divided medially into 2 hemitergites, each bearing a row of 4 spines. ... *Systemus* ... 4
 — R_{4+5} and M subparallel or M arched anteriorly; 'bosse alaire' absent; all ac aligned in two rows; usually 5 or fewer dc; antennae of both sexes similar, subrectangular to subovate, with apical arista; peduncle with tergum and sternum fused; female oviscapt without rows of spines. other Medeterinae
4. Antenna entirely black; coxa II with at least basal half dark brown. 5
 — Scape and pedicel yellow; coxa II almost entirely yellow (tropical Western Australia). Undescribed ♀ specimen
5. Coxa I, femur I yellow; surstylus concave, dish-like, with U-shaped excision guarded by 2 incurved setae; cercus bare along ventral margin (Fig. 3) (east. Australia). *S. australis*
 — Coxa I dark brown; femur I dark brown almost to apex; surstylus concave with excised curved wedge, distally with 2 ventrally directed curved pedunculate setae; cercus with ventral margin densely pubescent (Fig. 5) (south-west Western Australia). *S. curryi*

Systemus australis n. sp.

Figs 1-4, 6-7

Type material. HOLOTYPE σ : Australian Capital Territory: Black Mountain, 4-xii-1979, malaise site 1, D.H. Colless (ANIC). 6 PARATYPES: 1 σ , same data as holotype except 19-xi-1979 (ANIC). Queensland: 1 σ , Shipton's Flat, 15°47'S 145°14'E, 17-x-1980, malaise trap, D.H. Colless (ANIC); 1 σ , 15 km west of Irvinebank, 17°26'S 145°04'E, malaise trap, D.H. Colless (ANIC); 1 σ , 3 km north-east of Mt Webb, 15°03'S 145°09'E, 30-iv-1981, malaise trap, D.H. Colless (ANIC); 1 σ , Bellenden Ker Range, el. 100m, 17-x to 9-xi-1981, rainforest, Earthwatch/Queensland Museum (ANIC); 1 σ , Austral Forest via Bulburin, 24°34'S 151°29'E, Malaise trap site 3, 23-iii-1975, D.K. McAlpine (AMS).

Description. MALE: length 2.3-2.7 (Fig. 1).

HEAD: vertex, frons, face, dark metallic green with thick brownish pruinosity; clypeus dark blue-green with less pruinosity; palpi black with strong apical seta; proboscis brownish, projecting anteriorly, keel-like; mouthparts: labrum not elongated, epipharyngeal armature with two prongs, labium with 6 unsclerotised pseudotracheae, as in Group IV of Cregan (1941); anterior eye facets slightly enlarged; single row of strong pale postorbital setae becoming black near vertex; antenna black; pedicel short, with ring of apical setae; 1st flagellomere large, tapering, at least 3 times as long as basal width; densely pubescent; arista short, bare.

THORAX: dorsum metallic green with bronze reflections and thin grey pruinosity; bronze vittae over acrostichal band extending laterad along dorsocentral setae; pleura green with dense grey pruinosity; posterior third of mesonotum distinctly flattened; thoracic setae black; 12-14 pairs of acrostichals, of equal length except those of posterior pair bordering mesonotal depression, which are larger and offset laterad; 6 strong dorsocentrals, decreasing in size anteriorly with few short setae anteriorly; 2 pairs scutellars, laterals about $\frac{1}{2}$ length of medians; 1 pale proepisternal just above coxa I, subtended dorsally by shorter seta.

LEGS: coxa I yellow, coxae II, III dark brown basally, yellowish distally; remainder of legs yellow with only distal tarsomeres darkened; coxae I, II with pale anterior setae; coxa III with 1 strong pale lateral bristle; major leg setae black; relative proportions of podomeres given in the formula: femur; tibia; tarsomere 1/2/3/4/5; I: 4.0; 3.7; 2.0/1.2/0.7/0.5/0.5; II: 4.0; 4.5; 2.1/1.5/1.0/0.5/0.5; tibia II with strong anterodorsal (ad) and posterodorsal (pd) at $\frac{1}{4}$, the pd slightly basad of ad; a short pd at $\frac{3}{4}$ (sometimes indistinct); an irregular row of ventral setae projecting beyond vestiture; an apical ring of 4 strong bristles; III: 4.2; 5.7; 1.0/2.3/1.3/0.7/0.5; tibia III with row of 5-6 dorsal setae and 7-8 shorter ventral setae.

WING: dimensions 1.9-2.3 x 0.8-0.9; R_{2+3} and R_{4+5} diverging to wing apex; R_{4+5} and M bowed outwards subapically; anal vein and anal cell present; wing ratio (length cross vein m-cu/distal section CuA) somewhat variable: 0.4-0.7; lower calypter pale with black marginal setae; haltere yellowish.

ABDOMEN: metallic bronze-green with dusting of grey pruinosity; posterior margin of tergum 1 with row of long dark setae; terga 2-5 lacking ovoid depressions along lateral margin; sterna 2-6 membranous or only weakly sclerotised, somewhat recessed.

POSTABDOMEN: segment 7 forming elongate peduncle, glabrous, without setae; sternum and tergum 7 elongated, incompletely fused, separated by somewhat sclerotised pleural membrane, and sternum 7 somewhat twisted to right (Fig. 3); elongated external side of tergum 7 appearing V-shaped, representing posterior tergal margin; segment 8 represented by sternum only, forming cap-like covering over hypopygial foreamen on left side of epandrium (when postabdomen is retracted towards preabdomen, segment 7 is enfolded by terga 5 and 6, leaving only hypopygium visible; hypopygium (Figs 3,4) dark brown with yellowish surstyli and cerci; hypandrium an inverted trough, fused to epandrium, immovable (Fig. 4); aedeagus simple; 2 epandrial lobes, each bearing strong bristle, arising along lateral walls of genital chamber; surstyli not solidly fused to epandrium, but with line of weakness along join; in lateral view surstyli appearing as concave dish with U-shaped excavation behind 2 distinctive incurved setae, and bordered along ventral margin with mound of 6-7 strong setae, and with distal arm incurved medially bearing strong apico-ventral setae; cercus stout basally, tapering into long narrow arm with strong dorsal and apical setae, and bare along ventral surface.

FEMALE: length 2.1 (one specimen only). Similar to male except where noted: face slightly wider than in male; 1st flagellomere (Fig. 2) distinctly shorter, subovate; arista longer; wing dimensions 1.8 x 0.7; CuAx ratio: 0.5

ABDOMEN: segments 1-6 with well developed, sclerotised terga and sterna; lateral margins of terga 2-5 each with 3-4 ovoid depressions; segment 7 usually retracted under segment 6; segment 8 acting as struts for fused segments 9+10; terga 9+10 divided medially into 2 hemitergites, each bearing 4 spines and lateral seta; sterna 9+10 with setae as figured and with fused cercus (Figs 6, 7).

Remarks. The colouration of coxae II and III varies from dark brown only basally to almost entirely dark brown. The extent of darkening on the coxae may be a direct function of age. The tropical Queensland males are distinctly smaller (wing length 1.90-2.05) than the two Australian Capital Territory males (wing length 2.15, 2.30). The CuAx ratios appear to vary greatly (this ratio usually is fairly constant within species of dolichopodids), but this might be related to wing size: wing ratios Queensland males: 0.4-0.5; Australian Capital Territory males: 0.6, 0.7. Despite the size variation mentioned above, the male genitalia of all specimens are identical, and thus conspecific.

Systemus australis is found in various forested habitats along the coasts and ranges of eastern Australia, from tropical rainforests in northern Queensland to montane eucalypt woodland in the Australian Capital Territory. All specimens were taken in malaise traps.



Plate I

Figs 1-2. *Systemus australis*, Black Mtn, ACT: 1, male habitus, left lateral; 2, female antenna, left lateral.

Systemus curryi n. sp.

(Fig. 5)

Type material. HOLOTYPE, ♂: Western Australia: Crowea State Forest, near Pemberton, December, 1976, light trap, S.J. Curry (ANIC).

Description. MALE: length 2.1: (single male specimen mounted out of alcohol is somewhat shrunken and discoloured). Similar to male *S. australis* except as noted.

THORAX: dark metallic green with bronze vittae.

LEGS: all coxae dark brown, femur I dark brown to 'knee'; remainder of leg I, legs II and III entirely yellow except for darkened distal tarsomeres, leg chaetotaxy similar.

WINGS: dimensions 2.1 x 0.7; wing ratio: 0.7.

HYPOPYGIUM (Fig. 5): similar to *S. australis* except for details of surstyli and cercus; surstyli more compact, in lateral view with concave dish-like depression from which curved wedge is excised, and distally with 2 ventrally directed curved setae, dorsal seta on long pedicel, ventral seta on shorter pedicel; 3 strong setae arising from ventral side of depression; surstyli with ventral prominence and ventral setae as figured, with the distalmost setae distinctly hooked; cercus with ventral margin covered by dense hairs and lacking prominent apical setae.

FEMALE: unknown.

Remarks. This species was taken in the wet sclerophyll eucalypt forests of south-western Western Australia. *Systemus curryi* and *S. australis* have similar surstyli and cerci and, in comparison with genitalic figures of palearctic and nearctic species, appear to represent a natural species group. The presence of species pairs in the disjunct eucalypt forests of eastern Australia and south-western Western Australia is a common pattern in the Australian fauna (Keast, 1981). This pattern reflects increasing post-Miocene aridity which divided a once continuous southern Australian biota into a number of refugia, perhaps thereby facilitating allopatric speciation.

Other Australian *Systemus*

An isolated female *Systemus* sp. from tropical Western Australia (Drysdale River, 15°02'S 126°55'E, 3 to 8-viii-1975, ANIC) may represent a new species. Although it shows similarities to the *S. australis* female, its scape and pedicel are distinctly yellow and coxa II almost entirely yellow. Until it can be associated with a male, it remains undescribed.

Discussion

Because of similar sexually dimorphic antennae, species of *Systemus* were originally described in *Rhaphium* Meigen. Although *Systemus* was erected by Loew in 1857, the genus was long retained in the subfamily Rhaphiinae (e.g. Becker, 1917-18; Parent,

1938), despite obvious incongruities. The genus *Rhaphium* has a flat or convex dorsal postcranium, lacks a distinct fronto-clypeal suture, has 6 sclerotized pseudotracheae, an unflattened posterior part of the mesoscutum, coxa III with 2 external bristles, usually with abundant long hairs on the proepisternum near the anterior thoracic spiracle, and, most importantly, the hypopygium is encapsulated at the end of the abdomen with only a short internal segment 7. Robinson (1970) correctly removed *Systemus* from the Rhaphiinae and placed it as the sole representative of a new subfamily, the Systeminae. Ulrich (1981) accepted the Systeminae but claimed that a monogeneric subfamily was unsatisfactory. He tentatively placed the genera *Xanthina* Aldrich, *Achalcus* Loew, *Epithalassius* Mik and *Euxiphocerus* Parent in the subfamily because of similarity of habitus and antennal structure. I have examined specimens of the neotropical *Xanthina plumicauda* Aldrich and the presence of anterior preapicals on femora II and III, a dorsal arista, and a large encapsulated hypopygium of complex structure unlike *Systemus* would place it in the Peloroedinae or Xanthochlorinae of Robinson (1970). Descriptions and figures of *Achalcus* (Parent, 1938) and examination of New Zealand specimens which have been called *Achalcus* (Parent, 1933) would exclude this genus on the basis of anterior femoral preapicals and male postabdominal morphology. Figures of the male terminalia of the palearctic *Epithalassius* (Parent, 1938) and the afrotropical *Euxiphocerus* (Parent, 1935) would similarly exclude these two genera.

In summary, none of the additional genera Ulrich proposed for the Systeminae belong in the subfamily because of a distinctly different male postabdominal morphology. The genus *Systemus* is most closely allied to the Medeterinae as suggested by Robinson (1970) and discussed below.

Of the distinctive characters of *Systemus*, the following character states are ascribed (see Bickel, 1985 for further discussion).

A. Plesiomorphic character states with respect to the groundplan of the Dolichopodidae.

1. Eyes with tiny hairs between facets.
2. 'Bosse alaire' present, a flexion in the distal sector of wing vein M.
3. Anal vein present.
4. Female abdominal terga 9 + 10 divided medially, each hemitergite bearing a curved row of spine-like acanthophorites.

B. Synapomorphies (shared derived characters) with the subfamily Medeterinae.

1. Postcranium dorsally concave.
2. Femora II, III lacking anterior preapical bristles.
3. Segment 7 of male forming an elongate external peduncle for the hypopygium.
4. Two epandrial lobes present, each bearing a strong bristle.
5. Surstyli as only distal projection from epandrium.
6. Mesoscutum flattened posteriorly.
7. Larva associated with arboreal habitats (?)

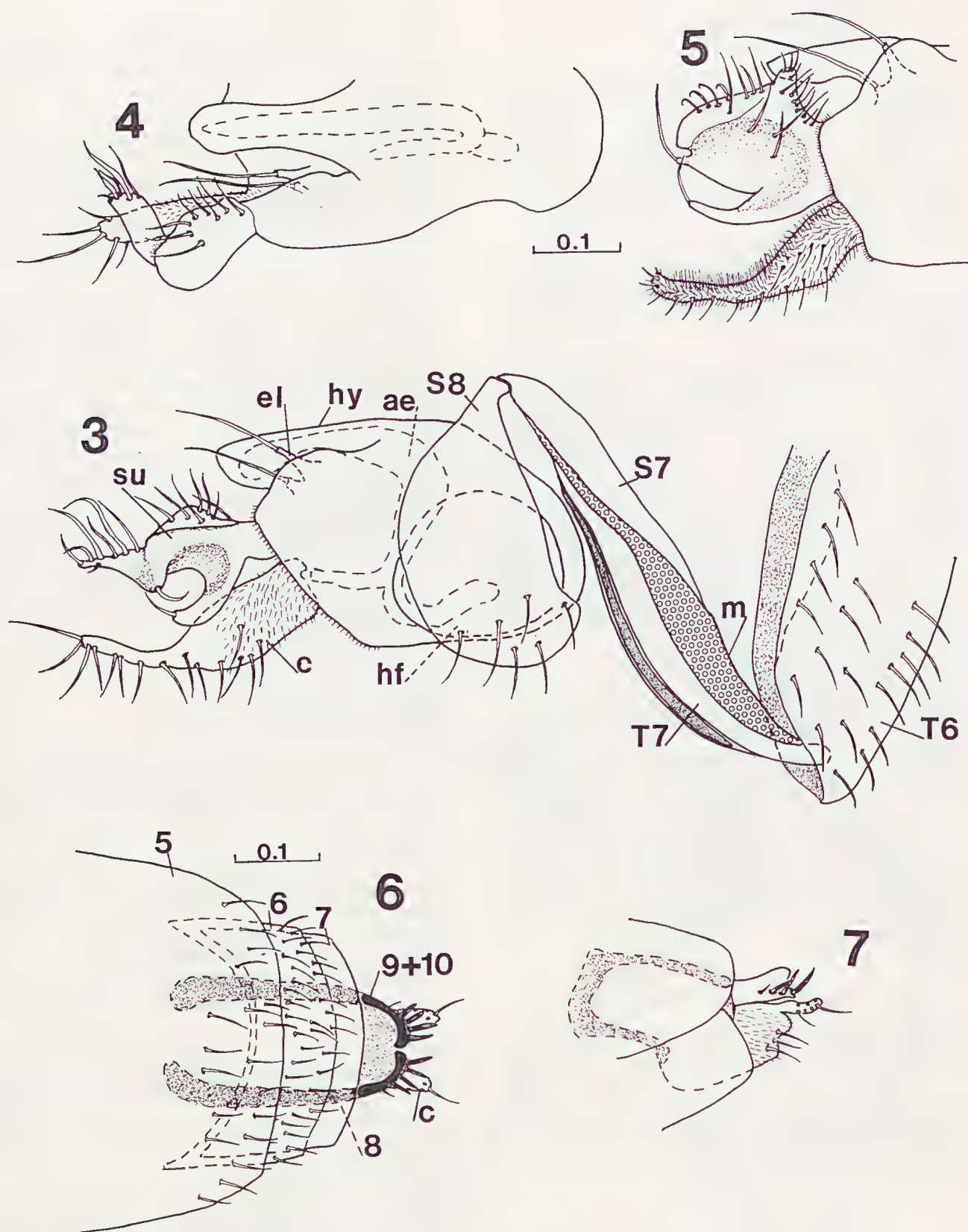


Plate II

Figs 3-4. *Systemus australis*: 3, male postabdomen, left lateral: S, sternum; T, tergum; ae, aedeagus; c, cercus; e.l., epandrial lobe; hf, hypopygial foramen; hy, hypandrium; m, pleural membrane; su, surstyli; 5, 6, etc., abdominal segments. 4, male hypopygium, ventral view, left side only.

Fig. 5. *Systemus curryi*, Crowea State Forest, WA, male hypopygium, left lateral, distal appendages.

Figs 6-7. *Systemus australis*, Mt Webb, Qld, female terminalia: 6, dorsal view; 7, lateral view.

C. Apomorphic characters shared with the subfamily Rhaphiinae, although probably homoplastic (convergent).

1. Antennae strongly sexually dimorphic, the male 1st flagellomere elongate tapering with short arista; female 1st flagellomere ovate with longer arista.

D. Autapomorphies

1. Thumb-like proleg on first abdominal segment of larva.
2. Posterior pair of acrostichals longer than preceding pairs and offset laterad.
3. Loss of ovoid depressions on the lateral margins of male abdominal terga.
4. Hypandrium fused to epandrium, immovable.

If the Medeterinae were interpreted to include the 'bosse alaire' in its groundplan, *Systemus* could easily be incorporated into the subfamily, perhaps as a separate tribe. The hypopygium of *Systemus* bears strong similarities to that of *Medetera* (see figures in Negrobov, 1971-77; and Bickel, 1985) with the presence of 2 bristle-bearing epandrial lobes, similar configuration and position of the surstyli (with no other distal epandrial appendages except the cerci), aedeagus with similar structure, internal curvature and formation of ejaculatory bulb, similar left lateral position of the hypopygial foramen, and similar form of the cerci. In addition, the relative proportions of the podomere segments are similar among *Systemus*, *Medetera* and *Thrypticus* (Medeterinae). A number of new medeterine genera await description and other included genera need redefinition before the position of *Systemus* within the Medeterinae can be ascertained. *Systemus* was the sole genus in the Systeminae (see Discussion, above), and since it is now included in the Medeterinae, there is no longer any need to maintain the subfamily Systeminae.

Additional Notes on *Systemus*

I have twice collected adult *Systemus* in North America (*S. eucenus* in New York State and *S. shannoni* in Maryland) as isolated individuals resting on tree trunks. They were orientated with head vertical, body parallel to the trunk. *Medetera* commonly rests on trunks in a similar manner. This habit of *Systemus* may provide further evidence for a link with the Medeterinae.

In a recent key to nearctic Dolichopodidae, (Robinson & Vockeroth, 1981), the second part of couplet 12, leading to *Systemus* + *Neurigona*, which states "tergite 7 mostly hidden, bare", does not hold for *Systemus*. Segment 7, the peduncle (formed of both tergum and sternum), will appear hidden only if retracted and enclosed by terga 5 and 6, whereas in *Neurigona*, it is always hidden. Also the tergum 7 of the nearctic *S. shannoni* is distinctly haired in specimens I have collected and in Fig. 3 of the original description (Wirth, 1953).

A useful generic key-character present in all specimens I have examined is the distinctly longer, laterally offset

posterior pair of acrostichals (ac). This character is present on both sexes and does not occur in genera usually keyed out with *Systemus*.

ACKNOWLEDGEMENTS. I wish to thank D.H. Colless, Australian National Insect Collection, Canberra (ANIC) and D.K. McAlpine, Australian Museum, Sydney (AMS) for the loan of specimens. Z. Liepa of the ANIC generously supplied photocopies of two journal articles.

References

- Becker, T., 1917-1918. Dipterologische Studien. Dolichopodidae. Nova Acta Academiae Caesareae Leopoldino Carolinae 102: 113-361; 103: 203-315; 104: 35-214.
- Bickel, D.J., 1985. A revision of the Nearctic *Medetera* (Diptera: Dolichopodidae). United States Department of Agriculture Technical Bulletin 1692: 1-109.
- Cregan, M.B., 1941. Generic relationships of the Dolichopodidae based on a study of the mouthparts. Illinois Biological Monographs 18: 1-68.
- Foote, R.H., J.R. Coulson & H. Robinson, 1965. Family Dolichopodidae. In "A Catalog of the Diptera of America North of Mexico" (A. Stone et al., editors). United States Department of Agriculture, Agricultural Handbook 276: 1-1696.
- Keast, A. (editor), 1981. Ecological biogeography in Australia. 3 vols. W. Junk, The Hague.
- Krivosheina, N.P., 1973. Larvae of the genus *Systemus* (Diptera: Dolichopodidae). Zoologicheskii Zhurnal 52: 1095-1097 (in Russian, English summary).
- Loew, H., 1857. Neue Beiträge zur Kenntnis der Dipteren Fünfter Beitrag. Königlichen Realschule zu Meseritz, Programm 1857: 1-56.
- Lundbeck, W., 1912. Diptera Danica, Part IV: Dolichopodidae. S. Gad, Copenhagen, 416 pp.
- McAlpine, J.F., 1981. Morphology and Terminology - Adults. In "Manual of Nearctic Diptera" (J.F. McAlpine et al., editors) Vol. 1: 9-64. Research Branch Agriculture Canada, Monograph 27, Ottawa, 674 pp.
- Negrobov, O.P., 1971-1977. Dolichopodidae, Unterfamilie Medeterinae. In "Die Fliegen der palaearktischen Region" (E. Lindner, editor) 29: 269-353, Lieferungen 284 (1971), 289 (1972), 302 (1974), 303 (1974), 316 (1977). Schweizerbart, Stuttgart.
- Parent, O., 1933. Étude monographique sur les Diptères Dolichopodides de Nouvelle Zélande. Annales de la Société scientifique de Bruxelles (B) 53: 323-441.
- 1935. Diptères Dolichopodides du Congo belge. Nouvelle contribution. Revue de Zoologie et de Botanique Africaines 27: 112-129.
- 1938. Diptères Dolichopodidae, Faune de France 35: 1-720.
- Robinson, H., 1970. The subfamilies of the family Dolichopodidae in North and South America (Diptera). Papéis Avulsos de Zoology, São Paulo 23(6): 53-62.
- Robinson, H. & J.R. Vockeroth, 1981. Dolichopodidae. In "Manual of Nearctic Diptera" (J.F. McAlpine et al., editors) Vol. 1: 625-639. Research Branch Agriculture Canada Monograph 27, Ottawa, 674 pp.

- Steyskal, G.C., 1970. Revisionary notes on the genus *Systemus* with a description of immature stages from tree cavities. *Proceedings of the Entomological Society of Washington* 72: 107-111.
- Ulrich, H., 1981. Zur systematischen Gliederung der Dolichopodiden (Diptera). *Bonner Zoologische Beiträge* 31: 385-402.
- Vaillant, F., 1978. Les *Systemus* et leur habitat dendrotelme (Dipt. Dolichopodidae). *Bulletin de la Société entomologique de France* 83(3-4): 73-85.
- Wirth, W.W., 1952. Three new nearctic species of *Systemus* with a description of their immature stages from tree cavities. *Proceedings of the Entomological Society of Washington* 54: 236-244.

Accepted 1st April 1986

Amphipoda from the South Pacific: Tonga

A.A. MYERS

Department of Zoology, University College,
Cork, Ireland

ABSTRACT. Thirty-two species of gammaridean Amphipoda are recorded from Tongatapu, Tonga. Five species are new to the Vanuatu-Tonga island arc, and these are figured, along with four other species. Seventy-two percent of the species collected are also known from Fiji. Two species are endemic to Tonga.

MYERS, A.A., 1986. Amphipoda from the South Pacific: Tonga. Records of the Australian Museum 38(5): 271-289.

Only four species of gammaridean amphipod appear to have been recorded from the Tonga island archipelago prior to the present work. All were collected by the U.S. Exploring expedition of 1838-42 and reported on by Dana (1853). Of these, one species, *Orchestia spinipalma* Dana (= *Talorchestia*) has since been recorded from the Bismark Archipelago, the Philippines, Australia and New Zealand, but the other three species (*Allorchestes gracilis* Dana, *Amphithoe tongensis* Dana and *Gammarus albidus* Dana) have not been recorded again either in Tonga or elsewhere, and even their identity remains equivocal.

The present work reports on a collection of gammaridean amphipods made by the writer on the island of Tongatapu, Tonga in 1979. Eleven families and thirty-two species are represented in the collection. Two species, *Lembos saloteae* Myers, described previously (Myers 1985a) from the same collection and *Parawaldeckia mua* Myers, are endemic. Seventy-two percent of the gammarideans represented in the collection are also known from Fiji. This might be anticipated, since the two archipelagos form part of the Vanuatu-Tonga island arc which originated at the mid Eocene/late Eocene boundary (c. 40 my BP).

Figures are given of the five species not previously recorded from the Vanuatu-Tonga island arc. Species described and figured from Fiji (Myers 1985c) are merely recorded (Table 1), except where significant variation is exhibited.

Specimens are housed in the author's personal collection and in the Australian Museum.

Of the 32 species in the Tongan material only *Amphilochus menehune* Barnard, *Gitanopsis tai* Myers, *Lembos saloteae* Myers and *Globosolembos excavatus* Myers have not been deposited in the Australian Museum.

Abbreviations Used in Figures

A1	Antenna 1
C1-2	Coxae 1-2
Epl-3	Epimera 1-3
G1-2	Gnathopods 1-2
Hd	Head
Md	Mandible Palp
P3-7	Pereopods 3-7
P7D	Dactylus of pereopod 7
Pl 1-4	Pleonites 1-4
Pr 6-7	Pereonites 6-7
T	Telson
Ul-3	Uropods 1-3.

FAMILY LEUCOTHOIDAE

Leucothoe hyhelia Barnard

Fig. 1

Leucothoe hyhelia Barnard, 1965: 489, fig. 5.—Barnard, 1970: 205, fig. 135.—? Ledoyer, 1978: 298.—? Ledoyer, 1979a: 102, fig. 63.

Remarks. Some doubt exists concerning the material attributed to this species by Ledoyer (1979a) from Madagascar. In that material, the palm of the hyperadult male gnathopod 2 propodus is distinctly toothed, the telson is distally simple and the peduncular articles of antenna 2 are elongate and slender. None of these character states were observed by Barnard (1965, 1970) nor were they exhibited by Tongan material. Material ascribed to *L. hyhelia* by Ledoyer (1978) from Mauritius was not figured, and in the light of the above comments must also remain unconfirmed.

Distribution. Hawaii, Tonga, ?Madagascar, ?Mauritius.

FAMILY ANAMIXIDAE

Paranamixis madagascarensis Ledoyer

Paranamixis bocki Ledoyer, 1967: 125, fig. 5c.—Ledoyer, 1978: 231, fig. 14 (not *P. bocki* Schellenberg, 1938).

Paranamixis madagascarensis Ledoyer, 1982: 141, fig. 49.—Myers, 1985c: 42, figs. 30–31.

Remarks. The *Leucothoides* form appears to be identical to that described from Fiji (Myers, 1985c) and attributed to *P. madagascariensis*. The *Leucothoides* material from Tonga is therefore assumed to be attributable to this species, but rearing of *Leucothoides* males through to hyperadult is required for confirmation.

FAMILY LYSIANASSIDAE

Parawaldeckia mua n. sp.

Figs 2–3

Type material. HOLOTYPE, ♀, 4.0 mm, AM P36954, Pangaimotu Island, among *Amphiroa* sp. on inner reef, 23 September 1979.

Description. Length, 4.0 mm. Eye large. Antenna 1 short, article 1 of peduncle not produced dorsodistally over article 2; article 3 of peduncle slightly telescoped into article 2; flagellum shorter than peduncle with 6 articles, accessory flagellum with 4 articles. Antenna 2 short, subequal in length with antenna 1, flagellum with 6 articles. Mandible palp, article ratios 5:12:10, article 3 weakly falcate and lacking terminal setae. Gnathopod 1 carpus and propodus subequal. Gnathopod 2 coxa over twice as long as broad; carpus and propodus

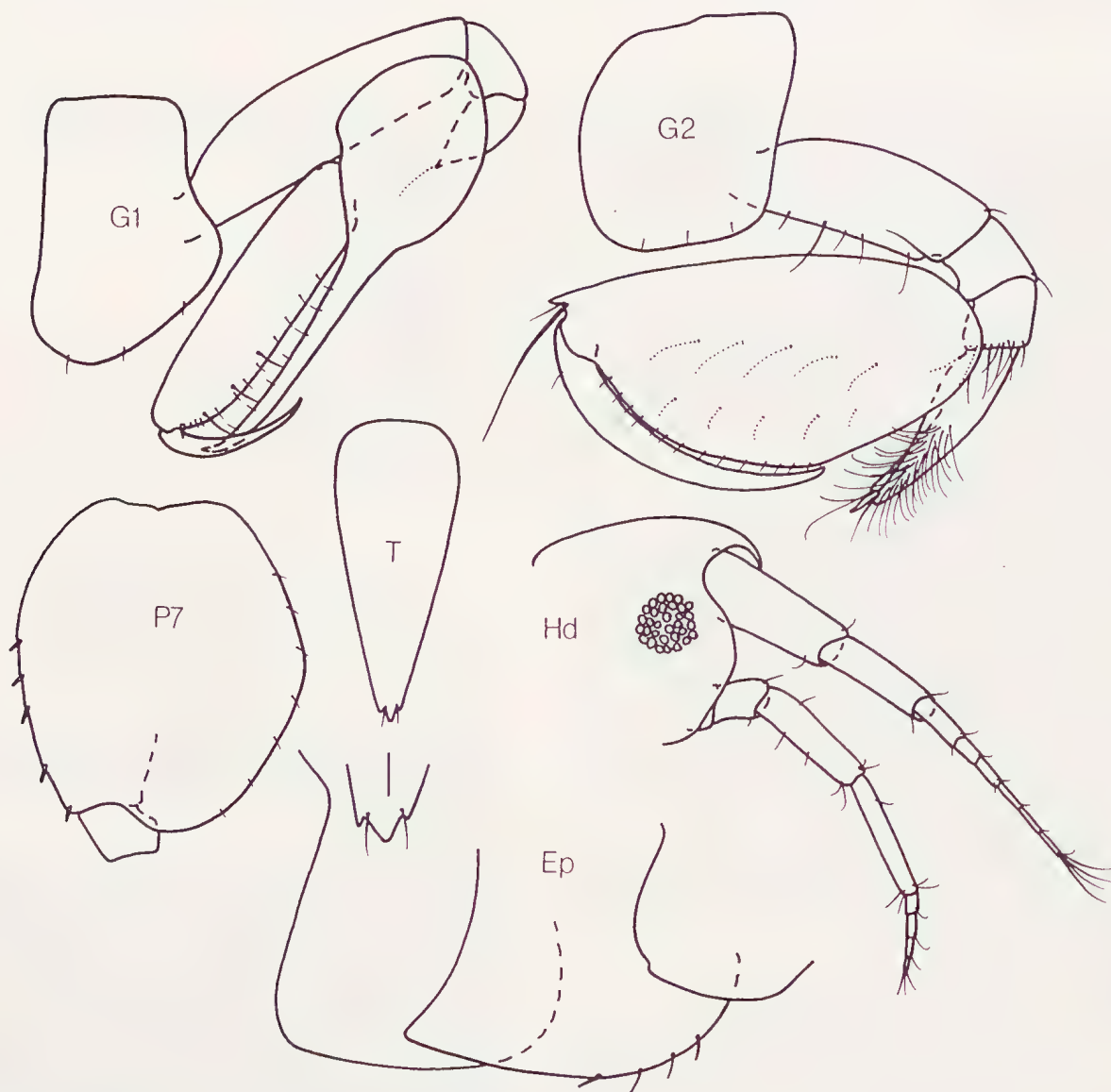


Fig. 1. *Leucothoe hyelia* Barnard, ♂ 2.5 mm, Utulau.

densely setose. Pereopod 5 basis grossly expanded, broader than long. Pereopod 7 basis slightly broader than long, posterior margin subrectangular, crenulate. Epimeron 3 evenly rounded. Uropod 1 outer ramus with two spines. Uropod 2 rami without spines. Uropod 3 peduncle greatly expanded; outer ramus with strong broad distal spine; inner ramus about half length of outer. Telson subsquare, with furled lateral margins.

Male unknown.

Remarks. *Parawaldeckia mua* is close to *P. lowryi* Myers and *P. dabita* Lowry and Stoddart. In the short antenna 2 and short inner ramus of uropod 3, *P. mua* is closest to *P. dabita*, however, the mandibular palp is most similar to *P. lowryi*. It differs from *P. dabita* in the strongly curved dactyls of pereopods 3–7 and less spinous uropods 1–2 as well as in the shape of the mandibular palp. Lowry (pers. comm.) considers *P. mua* to be closest to *P. lowryi*.

Distribution. Tongan endemic.

FAMILY MELITIDAE

Elasmopus alalo n. sp.

Figs 4–5

Elasmopus pseudaffinis.—Barnard, 1965: 501, figs 12–13.—Ledoyer, 1972: 219, pls 38, 39.—Ledoyer, 1978 (in part): 273, fig. 29A.—Berents, 1983: 118; figs 15–16.—Ledoyer, 1984: 65, fig. 30b. (not *E. pseudaffinis* Schellenberg, 1938: 53, fig. 25).

Type material. HOLOTYPE, ♂, 12.5 mm, AM P36955, Utulau, rock terrace. PARATYPES (57) AM P36956, same locality as holotype.

Description. Length 12.5 mm. Head with subocular notch. Eye subround. Mandible palp article 3 strongly

falcate, evenly setose on posterior margin. Antenna 1 and 2 setose; antenna 1 elongate, flagellum with about 32 articles; accessory flagellum multiarticulate. Gnathopod 1 coxa anterodistal corner produced forward, rounded; carpus and propodus subequal in length. Male gnathopod 2 coxa subtriangular; basis slender; merus with short acute posterodistal tooth; carpus short, anterior margin with one medial spine; propodus four times length of carpus, subrectangular, palm oblique, strongly spinose with deep, round bottomed excavation; dactylus strongly falcate, over half length of propodus. Female gnathopod 2 propodus one and a half times length of carpus and more than twice as long as broad, palm very oblique, defined by a spine. Pereopods 5–7 basis posterior margin smooth, but with fine setae. Pereopod 7 basis posteroproximal margin with 4–6 spines. Epimeron 3 with small tooth, but no notch. Uropod 3 rami subequal with short marginal spines. Telson apices sinuous, rounded, each lobe with two very small spines.

Remarks. Myers (1985c) questioned Barnard's (1965) and Berent's (1983) identifications of *E. pseudaffinis* from Micronesia and north-eastern Australia respectively and noted that Ledoyer (1978) had distinguished two "forms" of *E. pseudaffinis* from Madagascar and Mauritius. In the same paper, Myers (1985c) described from Fiji what he considered to be *E. pseudaffinis* Schellenberg, and suggested that the material of Barnard, Berents and Ledoyer (form 'A') probably represented a hitherto unrecognised species. Present material is ascribable to this new species and is given the name *E. alalo* n. sp.

Elasmopus alalo actually can now be seen to differ from *E. pseudaffinis* in a very large number of characters, principally the setose antennae, completely

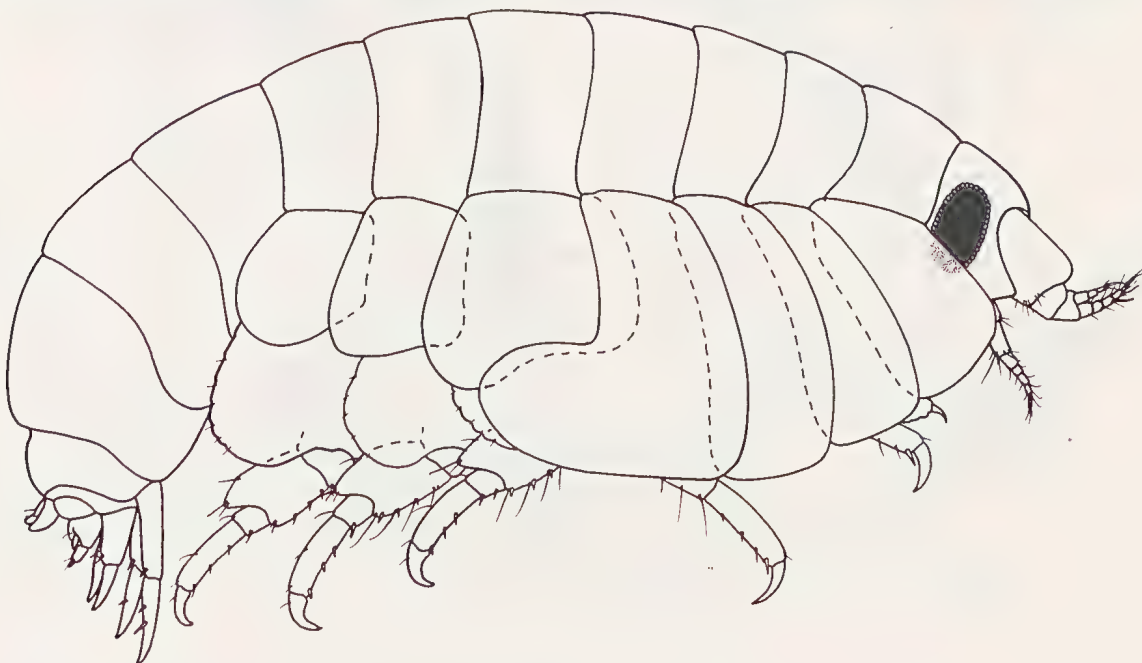


Fig. 2. *Parawaldeckia mua* n. sp., ♀ Holotype, 4.0 mm, Pangaimotu Island.

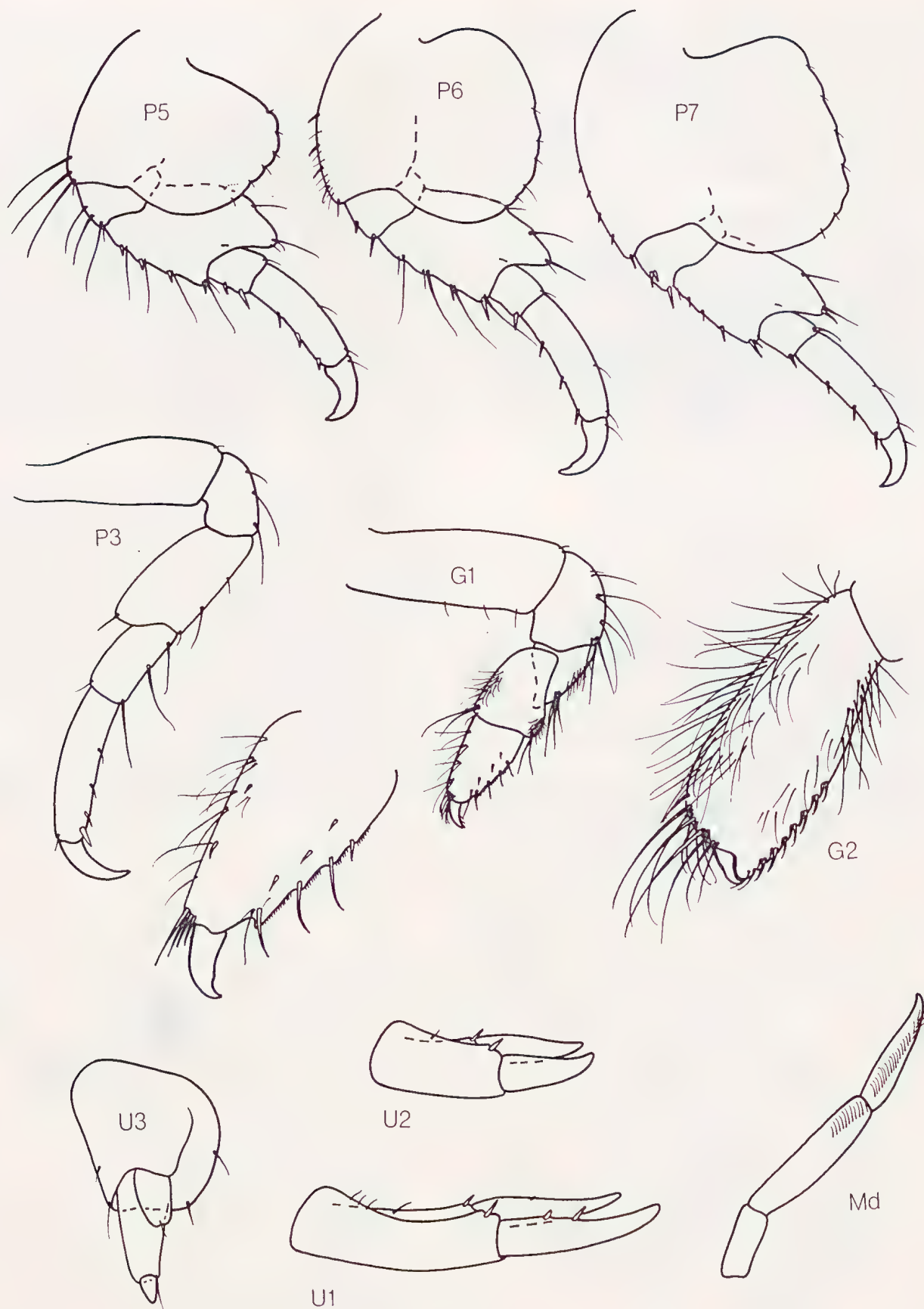


Fig. 3. *Parawaldeckia mua* n. sp., ♀ Holotype, 45.0 mm, Pangaimotu Island

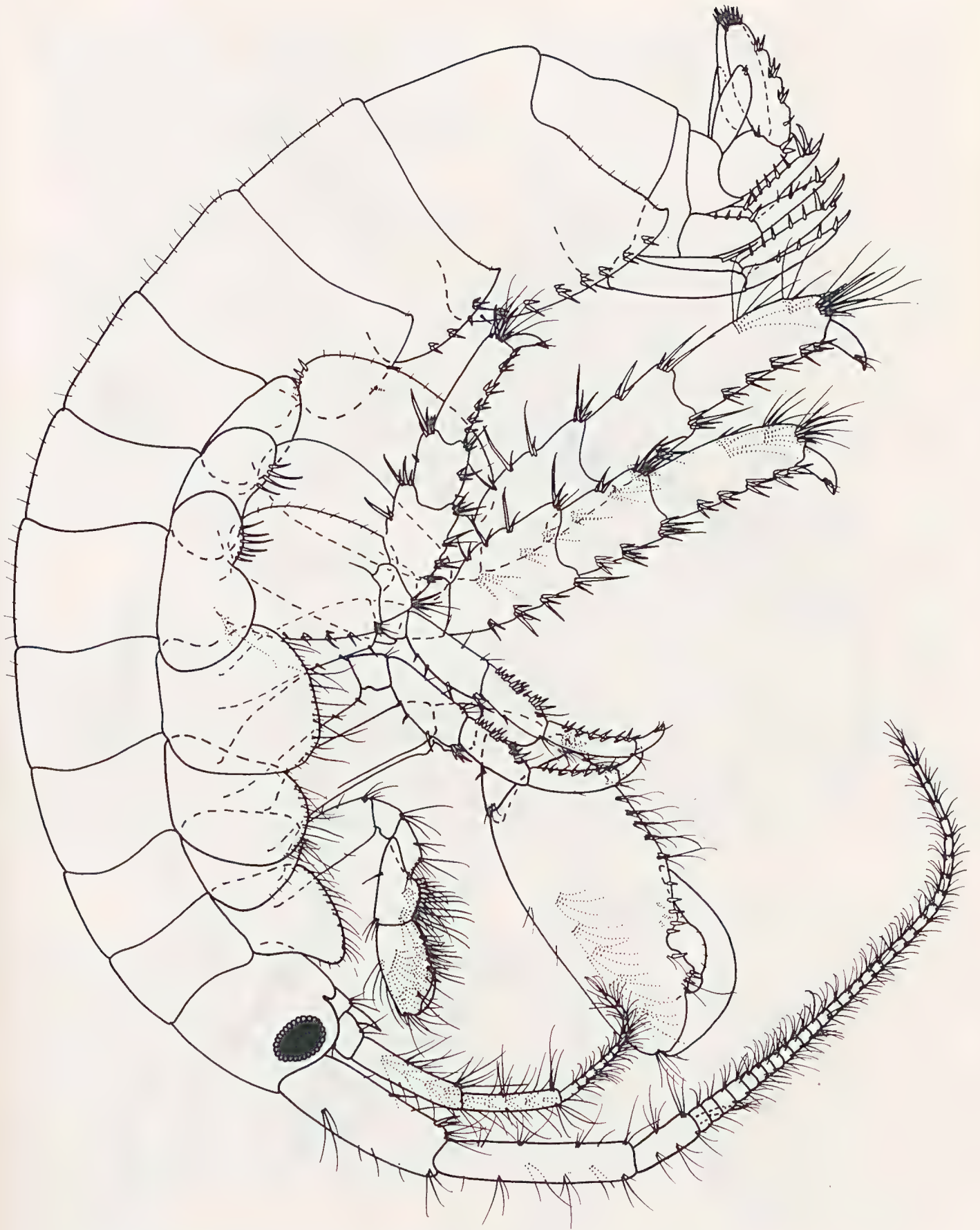


Fig. 4. *Elasmopus alalo* n. sp., ♂ 12.5 mm, Utulau.

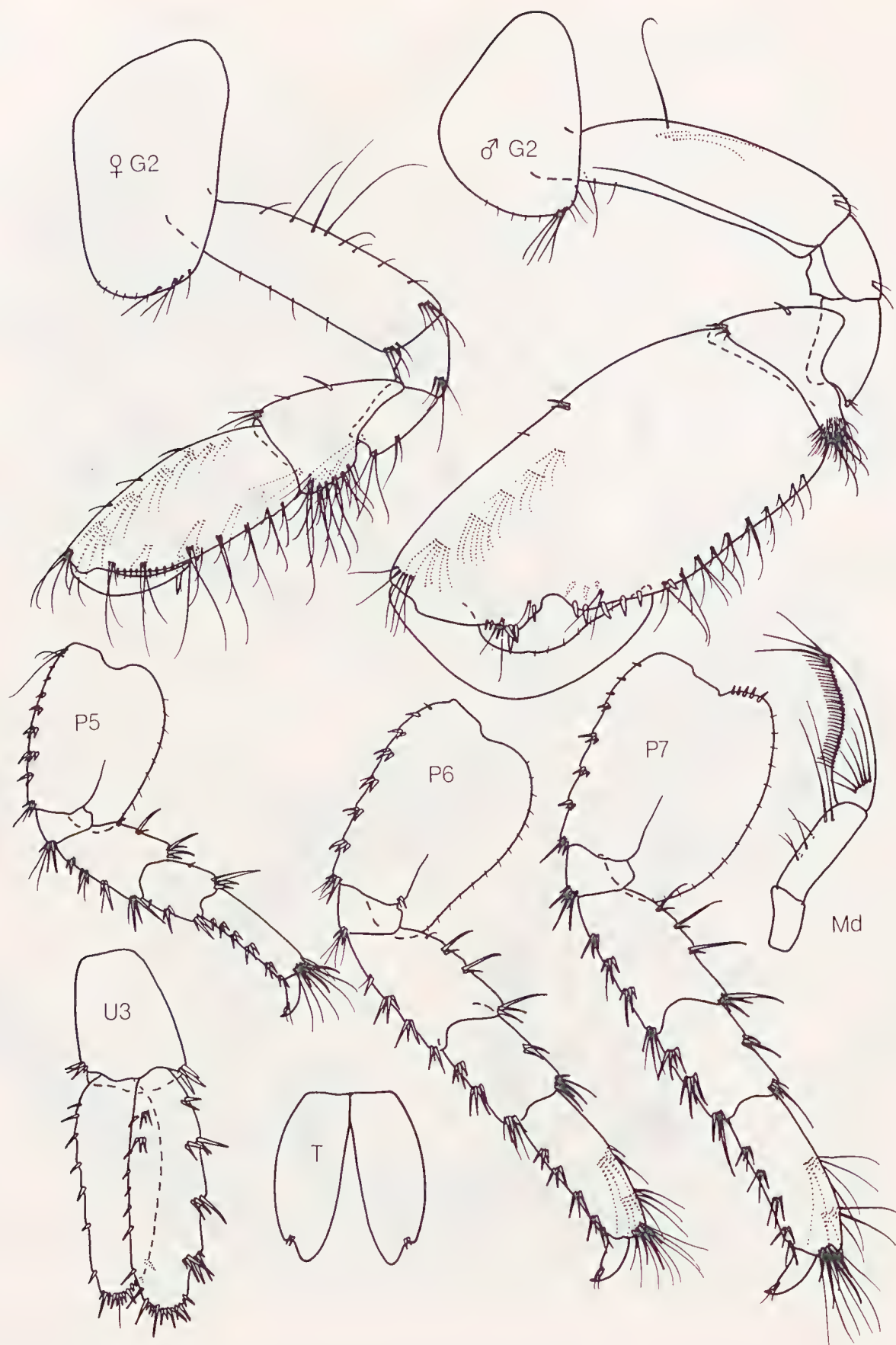


Fig. 5. *Elasmopus alalo* n. sp., ♂ 12.5 mm, ♀ 12.0 mm, Utulau.

different mandibular palp, non-acute coxa 1, subtriangular σ coxa 2 lacking spines, quite different σ gnathopod 2 (lacking spines on anterior margin of carpus, poorly produced merus, spinous palm of quite different shape, stout dactylus), non castellate pereopod 5–7 basis, short spined uropod 3 rami and telsonic apices. It is also a much larger species (12.5 mm as opposed to 6.0 mm in *E. pseudaffinis*).

Elasmopus gracilis Schellenberg

Figs 6–7

Elasmopus gracilis Schellenberg, 1938: 59, fig. 31.—Ledoyer 1967: 129, fig. 11.—Ruffo, 1969: 29, fig. 8.—Ledoyer, 1982: 488, fig. 176.

Remarks. Myers (1985c) noted the record of *E. gracilis* from Fiji (Schellenberg, 1938) but listed the species as requiring confirmation from that island group on the grounds that only females were recorded from there. The present record at least confirms the species from the Vanuatu-Tonga island arc and suggests that Schellenberg's Fiji record may have been correct.

Distribution. Red Sea, Madagascar, Ellice Islands, Tonga and probably Fiji.

Elasmopus molokai Barnard

Fig. 8

Elasmopus molokai Barnard, 1970: 120, figs 71–72.—Myers, 1985c: 102, fig. 82.

Elasmopus molokai (sic).—Ledoyer, 1984: 63, fig. 30a.

Remarks. Myers (1985c) pointed out that the Fijian material of this species differed from Hawaiian material in the presence of a tooth on the mediodistal excavation of the posterior margin of the male gnathopod 2 in some, but not all specimens. In the four Tongan males, this tooth is always present. For differentiating characters of this species and *E. hooheno* Barnard, see Myers (1985c).

Parelasmpus suensis (Haswell)

Fig. 9

Megamoera suensis Haswell, 1880: 335, pl. 21, fig. 5.

Parelasmpus suensis—Barnard, 1974: 143.—Berents, 1983: 138, figs 28–29.—Myers, 1985c: 126, figs 100–101.

Remarks. The genus *Parelasmpus* is badly in need of revision but sufficiently extensive materials are not yet available. Barnard (1974) documented what he considered to be major specific characters in the genus. These were: presence or absence of dorsal teeth on pereonite 7 in adults; nearly transverse or strongly oblique palm of male gnathopod 2; grossly or weakly serrate basis of pereopods 5–7; anteroventral tooth present or absent on coxa 1; and extremely long setae on pereopods 5–7.

In present material, pereopods 5–7 bear extremely long setae, only in hyperadult males. This does not

necessarily preclude this character state as a useful specific indicator, since it may be shown to occur in hyperadults of some but not all species. Nevertheless, it clearly shows that it is a character that must be used with caution when examining materials. Serration of the pereopod 5–7 basis is of dubious value since there appears to be gradation from fine to coarse toothing. Present material is somewhat intermediate in this respect. On the basis of pereon and pleon tooth formula, present material [pereonite 7 (2) pleonites 1 (2), 2 (2), 3 (0), 4 (1)] aligns itself with *P. suensis* (Haswell), *P. setiger* (Chevreux) and *P. suluensis* Stebbing (not Dana). It closely resembles material ascribed to *P. suensis* by Berents (1983) and Myers (1985c) but neither worker had hyperadult males present in their collections (Berents' material 6.8 mm, that of Myers 6.0 mm). Tongan males exhibiting densely setose pereopod 5–7 range from 8.0–10.0 mm.

Whether the three species mentioned above are synonymous cannot yet be ascertained [see Barnard (1974) for notes on *P. suensis* and *P. setiger*] but since *P. suensis* (Haswell) has priority that name is used herein for Tongan material.

Dana (1853) described and figured *P. albidus* (as *Gammarus albidus*) from Tongatapu, and makes no mention of paired teeth on pereon segment 7, although his figure indicates an angular posterodistal margin to segment 7. The small teeth on this segment could easily have been overlooked under the magnification of his hand lens. On the other hand, as pointed out by Barnard (1974) it is unlikely that he would have totally overlooked the serrations on pereopod 5–7 bases (which he figures as smooth). One is inclined to believe that Dana's Tongan material and present material from the same island is synonymous. This, however, would require the placing of *P. suensis* (Haswell) in the synonymy of *P. albidus* (Dana) which has priority. In order to prevent disruption in the present state of uncertainty, the position of *P. albidus* is left unresolved.

Mallacoota nananui Myers

Fig. 8

Elasmopus subcarinatus Chilton, 1915 (in part): 325, fig. 5. *Mallacoota subcarinata*—Barnard, 1972: 114, figs 59–60.—

Ledoyer, 1984: 72, fig. 34.

Mallacoota nananui Myers, 1985c: 121, fig. 95.

Remarks. This species is close to *M. latidactyla* Ledoyer, but differs in having article 2 of the mandibular palp longer than article 1, the telson more spinous and male gnathopod 2 with the posterior margin of the propodus sinuous not straight, the palm irregularly toothed, but never with deep round-bottomed excavation. In *M. latidactyla*, the deep palmar excavation remains unoccluded by the dactylus posterior margin when it is in the closed position and is presumably used for grooming the antenna 1.

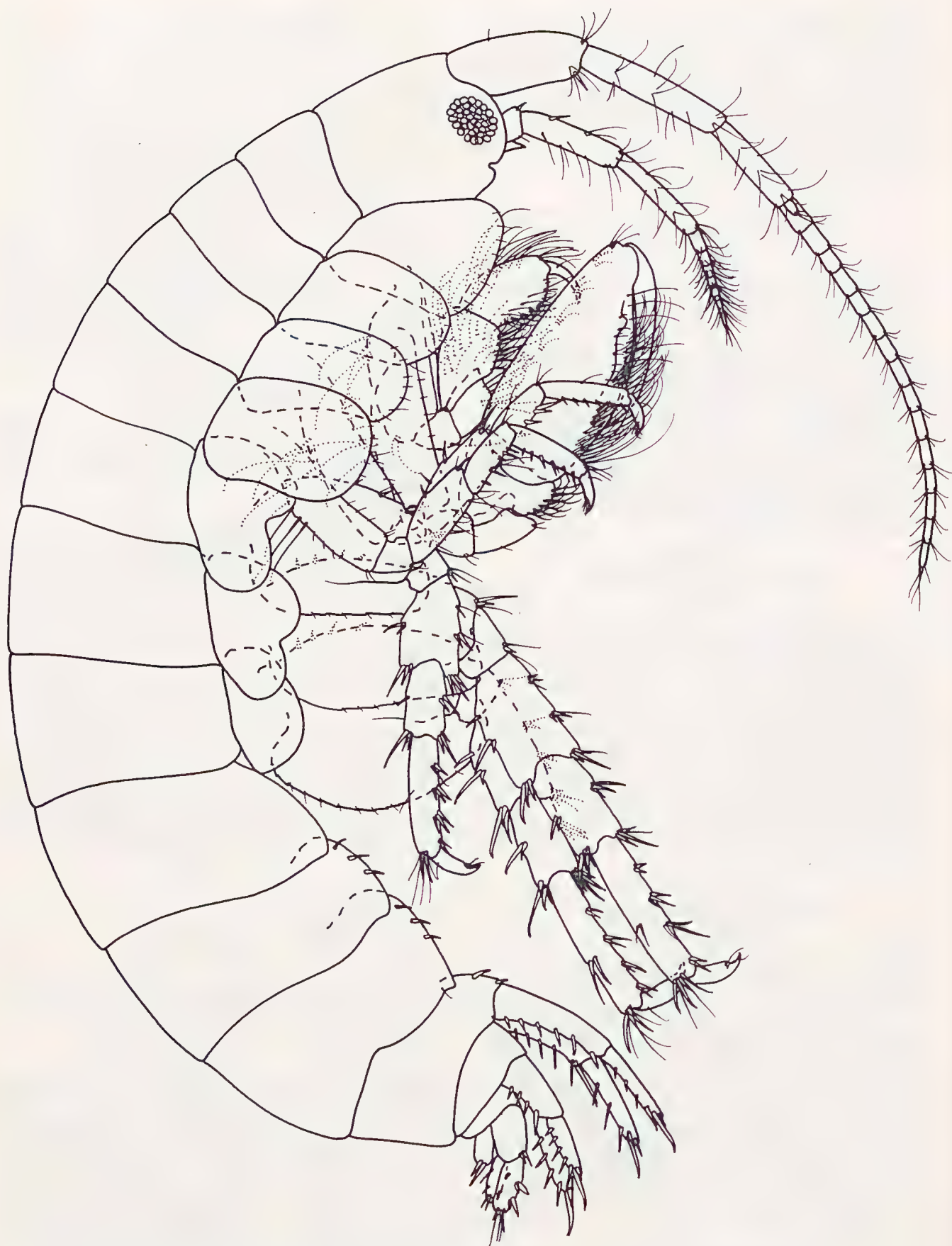


Fig. 6. *Elasmopus gracilis* Schellenberg, ♂ 4.0 mm, Utulau.

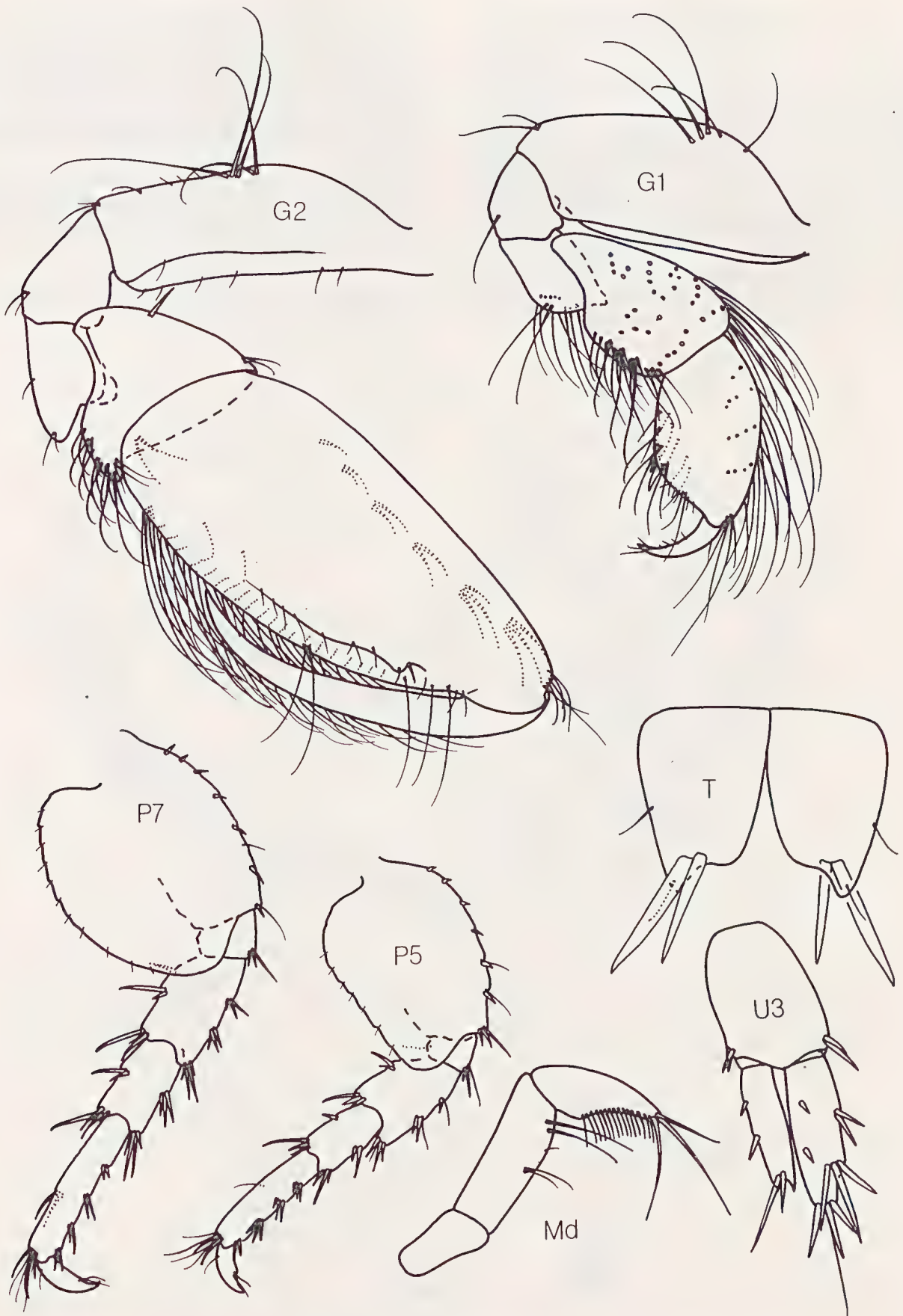


Fig. 7. *Elasmopus gracilis* Schellenberg, ♂ 4.0 mm, Utulau.

Eriopisella seychellensis (Chevreux)

Fig. 10

Eriopisa seychellensis Chevreux, 1901: 403, figs 19–23.—
Barnard, 1935: 284, fig. 4.

Remarks. Barnard (1970) described a new subspecies of *E. seychellensis* from Hawaii (*E. s. upolu*) which differed from the nominate subspecies by the “hands of the gnathopods” being slightly narrower, less ovate and more rectangular, the lateral cephalic lobes more strongly rounded, and the dactyls of pereopods 3–5 not bifid (= 5–7 in present terminology). Chevreux’s figure of an entire female is a little crude by modern standards, so that it is difficult to give weight to the significance

of head lobe shape and gnathopod proportions, although the enlarged figures of the gnathopoda do indicate a very broad gnathopod 2 carpus. The non bifid dactyls of the Hawaiian subspecies do seem significant. Present material has bifid dactyls on pereopods 5–7 and is therefore allocated for the moment to the nominate subspecies.

Ledoyer (1984) records *Eriopisella seychellensis upolu* from New Caledonia. He describes the dactylus of pereopods 5–7 as “simples”, but figures them bifid. Tongan and New Caledonia materials do not appear to differ significantly from one another.

Distribution. Seychelles, Hawaii, New Caledonia, Tonga (including subspecies).

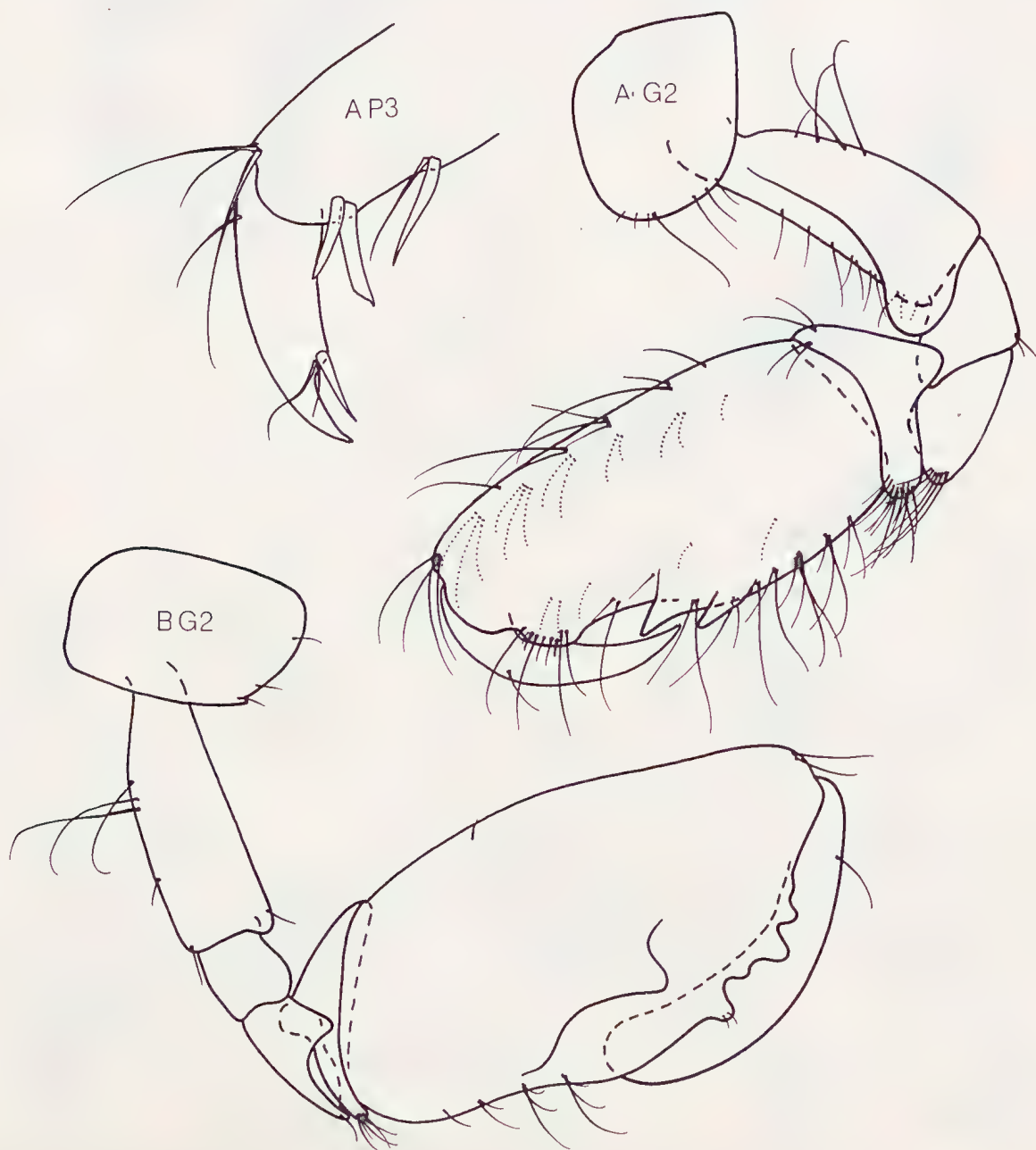


Fig. 8. A, *Elasmopus molokai* Barnard, ♂ 5.0 mm, Nukualofa; B, *Mallacoota nananui* Myers, ♂ 7.0 mm, Pangaimotu Island.

FAMILY AMPITHOIDAE

Cymadusa pilipes (Ledoyer) n. comb.*Paradusa bilobata pilipes* Ledoyer, 1984: 26, fig. 11.*Cymadusa lunata* Myers, 1985c: 33, figs 22-23.

Remarks. Myers (1985c) figured and described this species from Fiji, under the name *Cymadusa lunata*, but

concurrently, Ledoyer (1984) described the species from New Caledonia as a new subspecies of *Paradusa bilobata* Ruffo. The distinctive characters detailed by Ledoyer seem sufficient to warrant specific rank for this taxon, the name of which by priority must be *C. pilipes* (Ledoyer). Ruffo erected the genus *Paradusa* for a taxon with enlarged gnathopods 1 and 2 in the male, mandible palp with cylindrical articles and accessory flagellum with a single article. Conlon (1982) retained the genus *Paradusa*, and in her key to the genera of Ampithoidae,

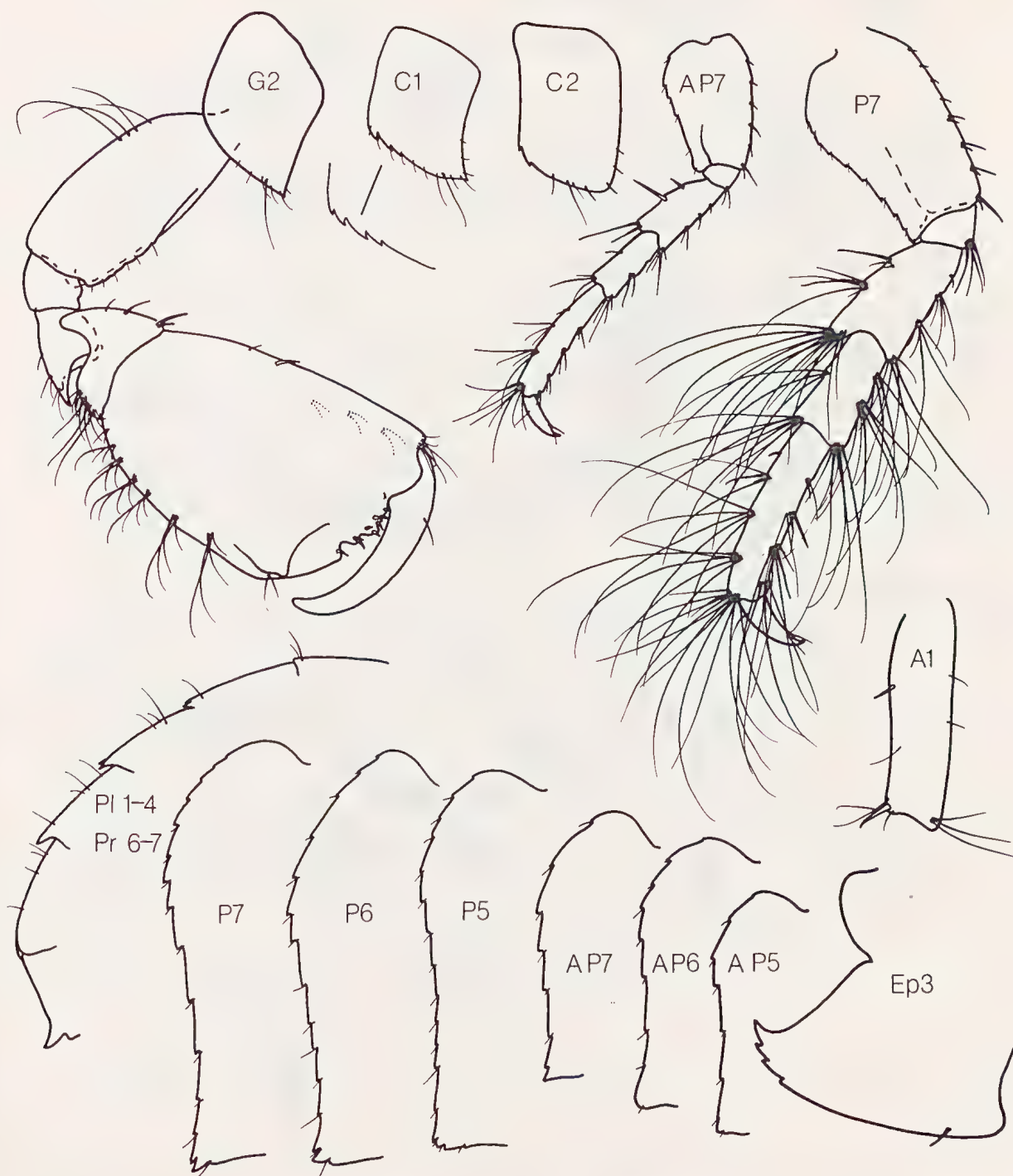


Fig. 9. *Parelasmopus suensis* (Haswell), ♂ 10.0 mm; A, ♂ 6.0 mm, Nukualofa.

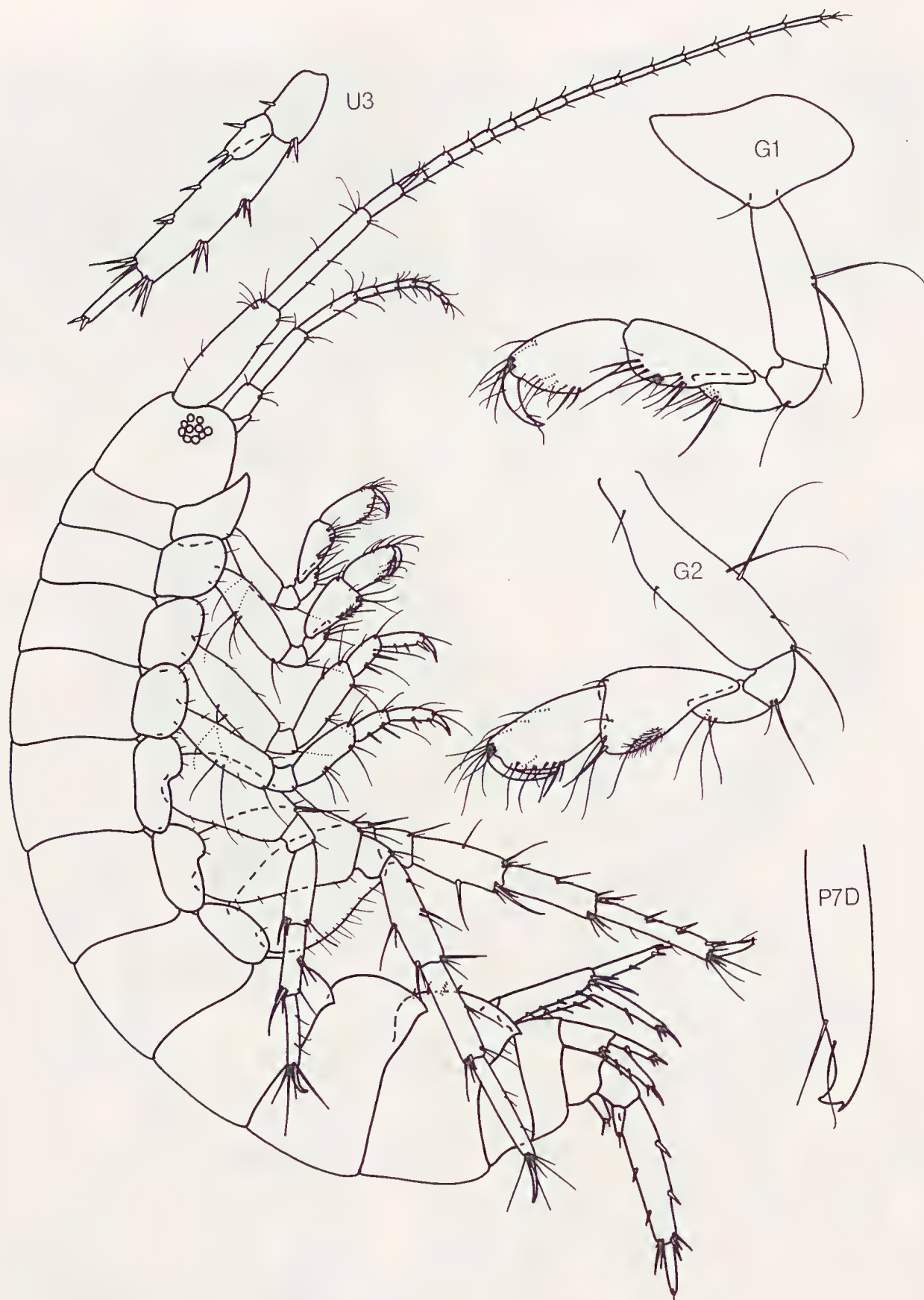


Fig. 10. *Eriopisella seychellensis* (Chevreux), ♀ 3.5 mm, Pangaimotu Island.

employed the same characters as those used by Ruffo (1969) in distinguishing *Paradusa* from *Cymadusa*. The reduction of one ramus of a biramus appendage is a phenomenon which is repeated again and again throughout the Crustacea. There is no reason to assume that the reduction of the accessory flagellum is a synapomorphy in Amphipoda. In any case, some species of *Cymadusa*, e.g. *C. brevidactyla*, also have an accessory flagellum composed of a single article. The mandibular palp article 3 of *C. pilipes* is not cylindrical but spatulate and the setae are not restricted to the tip as they are in the type species of *Paradusa*, *P. bilobata*. Indeed, the mandibular palp of *C. pilipes* does not differ from many *Cymadusa* species. Thus only the dual

enlargement of the male gnathopods 1 and 2 remains as a distinguishing feature between *Cymadusa* and *Paradusa*. Secondary enlargement of one pair of gnathopoda, to obscure a primary axial gradient, occurs quite often within corophioid genera and is a poor character upon which to base a genus. Female gnathopoda are generally plesiomorphic, lacking the complex secondary sexual modifications of males, and are good phylogenetic indicators. The female gnathopods of *C. pilipes* scarcely differ from those of *C. brevidactyla*. Detailed studies of mouthparts are needed to clarify the relationships of amphipod taxa, but at this stage there seems no valid basis for separating *C. pilipes* from its apparent congeners in *Cymadusa*.

FAMILY AORIDAE

Genus *Globosolembos* Myers

Eight species are currently known in the genus *Globosolembos* and, as pointed out by Myers (1985a), the identification of the species is difficult. Females are particularly difficult and in some cases cannot yet be separated. To aid in the identification of males in this species complex, a key to the species worldwide is given here.

Key to Male *Globosolembos* of the World

1. Gnathopod 1, palm defined by an acute tooth and a spine. *G. ruffoi*
 —Gnathopod 1, palm defined by a spine only or a spine and a rounded prominence or an excavation. 2
2. Mandibular palp article 3 longer than 2, posterior margin of article 3 concave. 3
 —Mandibular palp article 3 shorter than 2, posterior margin of article 3 convex. *G. tiafaui*
3. Gnathopod 1, palm with deep excavation. *G. excavatus*
 —Gnathopod 1, palm lacking deep excavation. 4
4. Gnathopod 1, palm evenly continuous with posterior margin. *G. francanni*
 —Gnathopod 1, palm distinguishable from posterior margin. 5
5. Gnathopod 1, palm sinuous with short convex portion and longer weakly concave portion. 6
 —Gnathopod 1, palm evenly convex except for short concave portion adjacent to rounded defining hump. *G. ovatus*
6. Sternal processes weak, rounded, epimeron 2 without long marginal setae. .. *G. indicus*
 —Sternal processes strongly produced, elongate on segments 2–3, epimeron 2 with long pectinate marginal setae. 7
7. Gnathopod 1, propodus one and a half times length of carpus. *G. leapakahi*
 —Gnathopod 1, propodus twice length of carpus. *G. smithi*

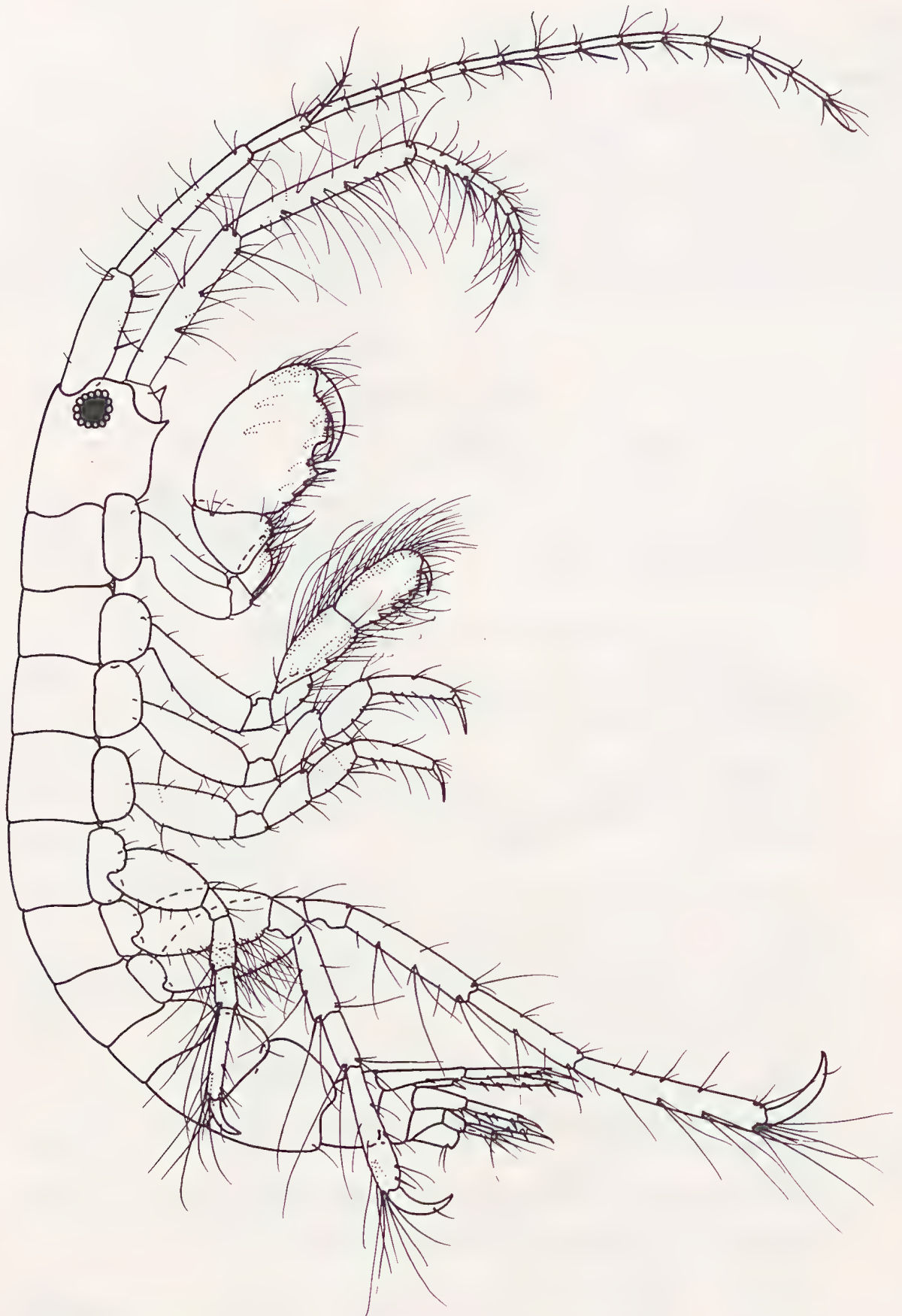


Fig. 11. *Globosolembos excavatus* Myers, ♂ 5.5 mm, Nukualofa.

Globosolembos excavatus Myers

Figs 11-12

Lembos excavatus Myers, 1975: 32, figs 76-82.—Ledoyer, 1982: 218, figs 104-105 (in part).

Lembos processifer.—Ledoyer, 1984: 35 (in part), fig. 16 ("forme 2").

Lembos (Globosolembos) excavatus Myers, 1985a: 363, fig. 234.

Remarks. Ledoyer (1984) has recently figured material from New Caledonia under the name *L. processifer* (Pirlot). He describes two forms under this name. Form 1 is distinctive and may indeed be *L. processifer*. The other, form 2, however, appears to be referable to *G. excavatus*.

Distribution. East Africa, Madagascar, N.E. Australia, New Caledonia, Tonga.

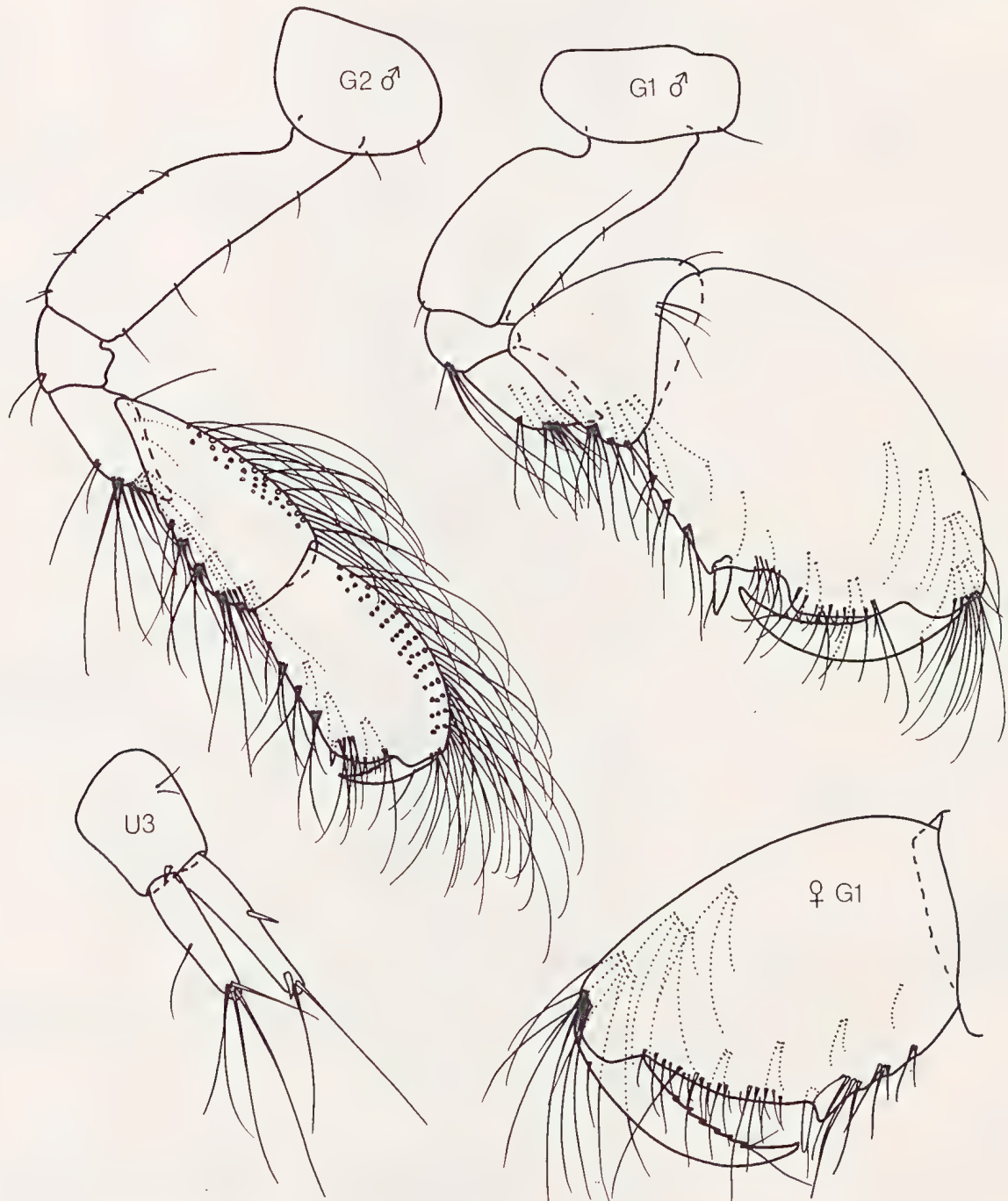


Fig. 12 *Globosolembos excavatus* Myers, ♂ 5.5 mm, ♀ 5.0 mm, Nukualofa.

Table 1. Annotated list of species recorded from Tonga.

Species	Locality	Tonga Habitat	♂	Material ♀	Imm	Distribution
AMPHILOCHIDAE						
<i>Amphilocheus menehune</i> Barnard, 1970	Nukualofa	Coral debris in lagoon		1		C
<i>Gitanopsis tai</i> Myers, 1985 c	Nukualofa	<i>Sargassum</i> sp. in lagoon		1		C
LEUCOTHOIDAE						
<i>Leucothoe hyhelia</i> Barnard, 1965	Nukualofa	Coral debris in lagoon		1		D
	Utulau	Coral debris and living <i>Acropora</i> sp. in lagoon	2	1		
<i>Leucothoella bannwarthi</i> Schellenberg, 1928	Pangaimotu Is.	<i>Amphiroa</i> sp. inner reef	1			C
ANAMIXIDAE						
<i>Paranamixis madagascarensis</i> Ledoyer, 1967	Pangaimotu Is.	<i>Amphiroa</i> sp. inner reef	2			C
<i>Paranamixis</i> form	Utulau	Coral debris and living <i>Acropora</i> sp. in lagoon	1			
<i>Leucothoides</i> form	Pangaimotu Is.	<i>Amphiroa</i> sp. inner reef		3		
	Nukualofa	<i>Sargassum</i> sp. in lagoon		1		
	Utulau	Mixed red algae on rock terrace		1		
HYALIDAE						
<i>Hyale chevreuxi</i> Barnard, 1916	Utulau	Mixed red algae on rock terrace	54	50		C
		Mixed red algae in lagoon	48	38		
		Mixed red/green algae in tide pool	2	2		
		Coral debris and living <i>Acropora</i> sp. in lagoon		1		
<i>H. galateae distorta</i> Myers, 1985c	Utulau	Mixed red algae on rock terrace	13	13		C
<i>Lelehua malevua</i> Myers, 1985c	Utulau	Mixed red algae on rock terrace	69	26		C
		Coral debris and living <i>Acropora</i> sp.	4	8		
		Mixed red algae in lagoon	148	32		
		Mixed red/green algae in tide pool	5	4		
EOPHLIANTIDAE						
<i>Bircenna dronga</i> Myers, 1985c	Utulau	Coral debris and living <i>Acropora</i> sp. in lagoon		1		C
		Mixed red/green algae in tide pool		1		
LYSIANASSIDAE						
<i>Parawaldeckia mua</i> n. sp.	Pangaimotu Is.	<i>Amphiroa</i> sp. inner reef		1		D
DEXAMINIDAE						
<i>Paradexamine rewa</i> Myers, 1985c	Pangaimotu Is.	<i>Heterozostera</i> sp. in lagoon		5		C
		<i>Amphiroa</i> sp. inner reef	5	12	61	
	Nukualofa	<i>Sargassum</i> sp. in lagoon	5	24		
		Coral debris in lagoon		1		
MELITIDAE						
<i>Elasmopus alalo</i> n. sp.	Utulau	Mixed red algae on rock terrace	26	42		D
	Utulau	Mixed red algae in lagoon	10	11		
		Mixed red/green algae in tide pool	1			

Species	Locality	Tonga Habitat	Material			Distribution
			♂	♀	Imm	
<i>E. gracilis</i> Schellenberg, 1938	Utulau	Mixed red algae on rock terrace	8	9		D
		Mixed red algae in lagoon	10	18		
		Mixed red/green algae in tide pool	11	13		
<i>E. lapu</i> Myers, 1985c	Utulau	Mixed red algae on rock terrace	7	10		C
		Coral debris and living <i>Acropora</i> sp. in lagoon	6	7		
		Mixed red algae in lagoon	3	1		
<i>E. molokai</i> Barnard, 1970	Pangaimotu Is.	<i>Amphiroa</i> sp. inner reef	2	1		C
	Nukualofa	Coral debris in lagoon	2	2		
<i>E. spinidactylus</i> Chevreux	Utulau	Mixed red algae on rock terrace	7	39		C
<i>Pareiasmopus suensis</i> (Haswell, 1880)	Pangaimotu Is.	<i>Amphiroa</i> sp. inner reef	5	12	6	C
	Nukualofa	Coral debris in lagoon	5	9		
		<i>Sargassum</i> sp. in lagoon		2		
<i>Mallacoota nananui</i> Myers, 1985c	Pangaimotu Is.	<i>Amphiroa</i> sp. inner reef	4	6		C
<i>Maera pacifica</i> Schellenberg, 1938	Pangaimotu Is.	<i>Amphiroa</i> sp. inner reef		1		C
	Utulau	Mixed red algae on rock terrace	3	7		
		Coral debris and living <i>Acropora</i> sp. in lagoon	1			
		Mixed red algae in lagoon		1		
<i>M. serrata</i> Schellenberg, 1938	Pangaimotu Is.	<i>Heterozostera</i> sp. in lagoon	1			C
	Nukualofa	Coral debris in lagoon	3			
	Utulau	Mixed red algae on rock terrace		1		
<i>Eriopisella seychellensis</i> (Chevreux, 1901)	Pangaimotu Is.	<i>Heterozostera</i> sp. in lagoon		1		D
AMPITHOIDAE						
<i>Paragrubia vorax</i> Chevreux, 1901	Utulau	Mixed red algae on rock terrace	10	16		C
		Coral debris in lagoon	2	3		
		Mixed red algae in lagoon	4	14		
<i>Cymadusa pilipes</i> (Ledoyer, 1984)	Pangaimotu Is.	<i>Heterozostera</i> sp. in lagoon	1	2		C
	Nukualofa	<i>Sargassum</i> sp. in lagoon	3	5		
		Coral debris in lagoon	5	6		
<i>C. brevidactyla</i> (Chevreux, 1907)	Pangaimotu Is.	<i>Heterozostera</i> sp. in lagoon		1		C
	Utulau	Mixed red algae on rock terrace	1	3		
		Coral debris and living <i>Acropora</i> sp. in lagoon		1		
		Mixed red algae in lagoon	4	8		
<i>Pleonexes kaneohe navosa</i> Myers, 1985c	Utulau	Mixed red algae on rock terrace	3	11		C
		Mixed red algae in lagoon	8	13		
<i>P. kulafi</i> Barnard, 1965	Nukualofa	<i>Sargassum</i> sp. in lagoon	1	3		C

Species	Locality	Tonga Habitat	♂	Material ♀	Imm	Distribution
<i>Ampithoe kava</i> Myers, 1985c	Nukualofa	<i>Sargassum</i> sp. in lagoon	5	17		C
ISAEIDAE						
<i>Gammaropsis digitata</i> (Schellenberg, 1938)	Pangaimotu Is.	<i>Heterozostera</i> sp. in lagoon		2		C
		<i>Amphiroa</i> sp. inner reef		4		
	Nukualofa	Coral debris in lagoon		1		
	Utulau	Mixed red algae on rock terrace	12	11		
		Mixed red algae in lagoon	2	2		
AORIDAE						
<i>Lembos aequimanus</i> Schellenberg, 1938	Pangaimotu Is.	<i>Heterozostera</i> sp. in lagoon	9	11	5	B
	Nukualofa	<i>Sargassum</i> sp. in lagoon	2	2		
		Coral debris in lagoon	2	2		
<i>L. dentischium taparum</i> Myers, 1985b	Pangaimotu Is.	<i>Amphiroa</i> sp. inner reef	8	13		B
	Nukualofa	Coral debris in lagoon	3	3		
	Utulau	Mixed red algae on rock terrace		1		
<i>L. saloteae</i> Myers, 1985b	Pangaimotu Is.	<i>Amphiroa</i> sp. inner reef	3	4		B
	Utualau	Mixed red algae on rock terrace		1		
<i>Globosolembos excavatus</i> Myers, 1985a	Nukualofa	Coral debris and <i>Sargassum</i> in lagoon	8	10		A

See A: Myers, 1985a B: Myers, 1985b C: Myers, 1985c D: Present paper.

References

- Audouin, V., 1826. In J.C. Savigny's 'Description de l'Egypte, Publiee par les ordres de sa Majeste l'Empereur Napoleon-le-Grand. Histoire Naturelle. Animaux articules'. Crustacees vol. 1, iv: 93, pl. II.
- Barnard, J.L., 1965. Marine Amphipoda of atolls in Micronesia. Proceedings of the United States National Museum 117 (3516): 459-552.
- 1970. Sublittoral Gammaridea (Amphipoda) of the Hawaiian Islands. Smithsonian Contributions to Zoology 34: 1-286.
- 1972. The marine fauna of New Zealand: Algae living littoral Gammaridea (Crustacea Amphipoda). New Zealand Oceanographic Institute Memoir 62: 1-216.
- 1974. Gammaridean Amphipoda of Australia, Part II. Smithsonian Contributions to Zoology 139: 1-148.
- Barnard, K.H., 1916. Contributions to the Crustacean fauna of South Africa, 5: The Amphipoda. Annals of the South African Museum 15: 105-302.
- 1935. Report on some Amphipoda, Isopoda and Tanaidacea in the collection of the Indian Museum. Records of the Indian Museum 37: 279-319.
- 1937. Amphipoda. In 'John Murray Expedition, 1933-34'. Scientific Report of the British Museum (Natural History) 4: 131-201.
- Berents, P.B., 1983. The Melitidae of Lizard Island and adjacent reefs. The Great Barrier Reef, Australia (Crustacea: Amphipoda). Records of the Australian Museum 35: 101-143.
- Chevreaux, E., 1901. Crustacés Amphipodes. Mission Scientifique de M. Ch. Alluaud aux Iles Séchelles (Mars, Avril, Mai, 1892). Mémoires de la Société Zoologique de France 14: 388-438.
- 1907. Diagnoses d'amphipodes nouveaux recueillis dans les possessions francaises de l'Océanie, par M.L. Seurat, Directeur du Laboratoire de recherches biologiques de Rikitea. Bulletin de Museum d'Histoire, Naturelle, Paris, 1907, 6: 412-417.
- 1908. Amphipodes Recueillis dans les Possessions Francaises de l'Océanie par M. le Dr. Seurat, Directeur du Laboratoire de Recherches Biologiques de Rikitea (Iles Gambier), 1902-1904. Memoire de la Société Zoologique de France 20: 470-527.
- Chilton, C., 1915. The New Zealand species of the amphipodan genus *Elasmopus*. Transactions and Proceedings of the New Zealand Institute 47: 320-330.
- Conlon, K.E., 1982. Revision of the gammaridean amphipod family Ampithoidea using numerical analytical methods. Canadian Journal of Zoology 60 (8): 2015-2027.
- Dana, J.D., 1853-55. Crustacea. Part II. United States Exploring Expedition 14: 689-1618, atlas of 96 pls.
- Griffiths, C.L., 1973. The Amphipoda of Southern Africa.

- Part I. The Gammaridea and Caprellidea of Southern Mozambique. *Annals of the South African Museum* 60 (10): 265–306.
- 1976. Some new and notable Amphipoda from Southern Africa. *Annals of the South African Museum* 72 (2): 11–35.
- Haswell, W.A., 1880. On some additional new genera and species of amphipodous crustaceans. *Proceedings of the Linnean Society of New South Wales* 4: 319–350.
- Ledoyer, M., 1967. Amphipodes gammariens des herbiers de phanerogammes marines de la région de Tulear (Republique Malgache) étude systématique et écologique. *Annales de la Faculté des Sciences de l'Université de Madagascar* 5: 121–170.
- 1972. Amphipodes gammariens vivant dans les alvéoles des constructions organogènes récifales intertidales de la région de Tulear (Madagascar). *Tethys Supplement* 3: 165–286.
- 1973. Amphipodes gammariens de la frondaison des herbiers *D'Enhalus* de la région de Nosy-be (Madagascar). Comparaison avec la faune des herbiers de Tulear. *Tethys Supplement* 5: 25–36.
- 1978. Amphipodes gammariens (Crustacea) des biotopes cavitaires organogènes récifaux de l'île Maurice (Océan Indien). *The Mauritius Institute Bulletin* 8 (3): 197–332.
- 1979a. Expedition Rumphius II (1975). Crustacés parasites, commensaux etc. VI. Crustacés Amphipodes Gammariens. *Bulletin du Museum National d'Histoire Naturelle*, Paris, 4^{er} ser. 1 (1): 137–181.
- 1979b. Les gammariens de la Pente externe du grand récif de Tulear (Madagascar) (Crustacea Amphipoda). *Memorie del Museo Civico di Storia Naturale di Verona* (2nd Ser.) 2: 1–150.
- 1982. Crustacés Amphipodes Gammariens Famille des Acanthonotozomatidae à Gammaridae. *Faune de Madagascar* 59 (1): 1–598.
- 1984. Les gammariens (Crustacea, Amphipoda) des herbiers de phanerogames marines de Nouvelle Calédonie (région de Neumea). *Memoires du Museum National d'Histoire Naturelle A, Zoologie*, 129: 1–113.
- Myers, A.A., 1975. Studies on the genus *Lembos* III: Indo-Pacific species. *L. kidoli* sp. nov., *L. ruffoi* sp. nov., *L. excavatus* sp. nov., *L. leptochirus* Walker. *Bulletino del Museo Civico di Storia Naturale*, Verona 2: 13–50.
- 1985a. Studies on the genus *Lembos* XI: *Globosolembos* sub-gen. nov., *L. (G.) francanni* Reid, *L. (G.) indicus* Ledoyer, *L. (G.) ovatus* sp. nov., *L. (G.) tiafaui* sp. nov., *L. (G.) excavatus* Myers. *Bolletino del Museo Civico di Storia Naturale*, Verona 10: 341–367.
- 1985b. Studies on the genus *Lembos* XII: Tropical Pacific Islands. *L. dentischium* Myers ssp. *taparum* nov., *L. saloteae* sp. nov., *L. waipio* Barnard, *L. aequimanus* Schellenberg, *L. virgus* sp. nov., *L. regius* sp. nov., *L. tui* sp. nov. *Bolletino del Museo Civico di Storia Naturale*, Verona 10: 369–406.
- 1985c. Shallow-water, Coral Reef and Mangrove Amphipoda (Gammaridea) of Fiji. *Records of the Australian Museum Supplement* 5: 1–143.
- Pirlot, J.M., 1938. Les amphipodes de l'expédition du Siboga. Deuxième Partie: III (2): Dexaminidae-Podoceridae. *Siboga Expeditie, Monographie* 33f: 329–359.
- Rabindranath, P., 1972. Marine Gammaridea (Crustacea, Amphipoda) from the Indian region. Family Ampithoidae. *Marine Biology* 14 (2): 161–178.
- Ruffo, S., 1969. Studi sui Crostacei anfipodi LXVII. Terzo Contributo alla conoscenza degli anfipodi del mar Rosso. *Memorie del Museo Civico di Storia Naturale*, Verona 17: 1–77.
- Schellenberg, A., 1928. Report on the Amphipoda. In 'Zoological Research Cambridge Expedition Suez Canal, 1924'. *Transactions of the Zoological Society of London* 22: 633–692.
- 1938. Littorale Amphipoden des Trokischen Pazifics. *Kungliga Svenska Vetenskapsakademiens Handlingar*, ser. 3, 16: 1–105.
- Schoemaker, C.R., 1942. Amphipod crustaceans collected on the Presidential Cruise of 1938. *Smithsonian Miscellaneous Collections* 101 (11): 1–52.
- Sivaprakasam, T.E., 1966. Amphipoda from the east coast of India. Part 1. Gammaridea. *Journal of the Marine Biological Association of India* 8 (1): 82–122.
- 1968. Amphipods of the genera *Maera* Leach and *Elasmopus* Costa from the East coast of India. *Journal of the Marine Biological Association of India* 10 (1): 34–51.
- 1970a. Amphipoda from the East coast of India. Part 2. Gammaridea and Caprellidea. *Journal of the Bombay Natural History Society* 66 (3): 560–576.
- 1970b. Amphipods of the family Ampithoidae from the Madras coast. *Journal of the Marine Biological Association of India* 12 (1–2): 64–80.
- Stebbing, T.R.R., 1899. Amphipoda from the Copenhagen Museum and other sources. Part II. *Transactions of the Linnean Society of London* 7 (8): 395–432.
- Walker, A.O., 1909. Amphipoda Gammaridea from the Indian Ocean, British East Africa, and the Red Sea. *Transactions of the Linnean Society of London series 2, Zoology* 12: 323–344.

Accepted 19th June 1986

RECORDS OF THE AUSTRALIAN MUSEUM

VOLUME 38 No. 6

Australian Thaumaleidae (Insecta: Diptera)	G. THEISCHINGER	291
The Polycirrinae (Polychaeta: Terebellidae) from Australia	PAT HUTCHINGS & CHRIS GLASBY	319
Some majid spider crabs from the deep Indo-West Pacific	D.J.G. GRIFFIN & H.A. TRANTER	351

Australian Thaumaleidae (Insecta: Diptera)

G. THEISCHINGER

20 Leawarra Street,
Engadine, NSW 2233, Australia

ABSTRACT. For the first time Thaumaleidae from Australia are named and classified. They are placed in two genera, *Austrothaumalea* Tonnoir and *Niphta* n. gen. The following new species are described: *Austrothaumalea australis* n. sp., *A. barrydayi* n. sp., *A. capricornis* n. sp., *A. cervulus* n. sp., *A. commoni* n. sp., *A. denticulata* n. sp., *A. fusca* n. sp., *A. macalpinei* n. sp., *A. minnamurrae* n. sp., *A. similis* n. sp., *A. simplex* n. sp., *A. sinuosa* n. sp., *A. spinosa* n. sp., *A. tasmanica* n. sp., *A. tonnoiri* n. sp., *A. uptoni* n. sp., *A. victoriae* n. sp., *A. zentae* n. sp., *Niphta bickeli* n. sp., *N. collessi* n. sp., *N. farecta* n. sp. A key is given to the males of all recognized Australian species and to the females so far as identifiable. New combinations are *Niphta halteris* (Edwards) and *Niphta nudipennis* (Edwards) from South America, both originally described under *Austrothaumalea*.

THEISCHINGER, G. 1986. Australian Thaumaleidae (Insecta: Diptera). Records of the Australian Museum 38(6): 291–317.

The Thaumaleidae comprise a homogeneous family of small (wing length 1.5–7.5 mm) (Fig. 1) stoutly built flies with shiny yellow to black bodies. Their eyes are holoptic in both sexes, their antennae short and slender. The wings have a characteristic venation and tend to fold downwards across a transverse line of weakness near the apex of the subcosta. The adults are diurnal and usually frequent wet rocks or vegetation near streams in wet forest. The larvae are aquatic and amphipneustic. The family (about 100 described species) is possibly mainly holarctic in distribution with less than a dozen species having been described previously from the southern hemisphere.

Tonnoir (1927) was the first to record Thaumaleidae from Australasia. He described a new genus, *Austrothaumalea*, with two species, *A. neozealandica* Tonnoir and *A. appendiculata* Tonnoir, from New Zealand. Tonnoir (1927) also recorded *Austrothaumalea* from Australia (including Tasmania) and announced the description of eight species from this region. However, Tonnoir published no descriptions of Australian members of *Austrothaumalea*. Referring to Tonnoir (1927) several authors (e.g. Edwards, 1929, 1930; Stuckenberg, 1960, 1961; Stone, 1966; Colless &

McAlpine, 1970; Arnaud, 1977; McLellan, 1983) mentioned the existence of undescribed species of *Austrothaumalea* in Australia. Of these, only Colless & McAlpine (1970) were more specific. They regarded the Australian species of Thaumaleidae as belonging to *Austrothaumalea* with one exception which appeared to be a member of the South African genus *Afrothaumalea* Stuckenberg.

Materials and Methods

For this paper I have studied all Australian Thaumaleidae made available from the Australian National Insect Collection (ANIC) in Canberra (which also holds Tonnoir's unpublished notes and collection), from the Australian Museum (AM) in Sydney, from the Museum of Victoria (MV) in Melbourne, and my own material (GT). This enabled me to present descriptions of 21 species. Whereas 18 belong to *Austrothaumalea*, 3 represent a new genus, perhaps close to but different from *Afrothaumalea*. The available larvae agree morphologically with the description which McLellan (1983) gave for *A. neozealandica* but cannot be specifically identified. From comparing the area covered

by collecting and the area presumably suitable for Thaumaleidae in Australia, more species and considerable extensions of the known distributions must be expected.

Illustrations of wings and descriptions of colouration are given from dry specimens. The descriptions and illustrations of the genitalia are based on material cleared in KOH. The wings of all species are more or less hyaline. The colour given in the descriptions is, therefore, that of the infuscation of the membrane and of the venation which is less transparent. The terminal segment of the male is mostly slightly paler than the rest of the abdomen. The aedeagus of *Austrothaumalea* is a very delicate and complex structure; my illustrations and descriptions only cover the more strongly sclerotized

portions of the aedeagus as detectable from ventral view without distorting the remainder of the genitalia. The sexes have been associated with each other by various ways of exclusion (geographic, venational, size, colour). The terminology used follows Colless & McAlpine (1970) for the wing venation, and McLellan (1983) for the genitalia (see Figs 13–15, 109–111).

The abbreviations of institutions housing material examined have been given above. Other than these and standard abbreviations the following abbreviations have been used:

c.u. collector(s) unknown
nr near
same loc. same locality.

Key to Genera and Species of Australian Thaumaleidae

1. No ridge in front of wing base (Fig. 35); transverse section of R_2 closer to the end of R_{1+2} than to the origin of R_{2+3} ; R_{4+5} arched posteriorly (e.g. Fig. 36). *Austrothaumalea* ... 2
- Prominent ridge in front of wing base (Fig. 103); transverse section of R_2 markedly closer to origin of R_{2+3} than to end of R_{1+2} ; R_{4+5} arched anteriorly (e.g. Fig. 97). *Niphta* ... 31
2. R_{4+5} with macrotrichia. *A. tasmanica*
- R_{4+5} without macrotrichia. 3
3. R_3 very slightly sinuous, appendix of CuA + 1A very substantial (e.g. Fig. 17); thorax very dark (blackish). 4
- Combination of wing and colour features otherwise. 6
4. Dististyles simply bent (Fig. 37); Tasmanian species. *A. fusca*
- Dististyles 2-branched (e.g. Fig. 18); mainland species. 5
5. Outer branch of dististyles substantial, more than half as long as inner branch (Fig. 20); known from Blue Mountains and coast near Sydney. *A. cervulus*
- Outer branch of dististyles minute, less than $\frac{1}{4}$ length of inner branch (Fig. 85); known from Clyde Mountain only. *A. uptoni*
6. CuA + 1A straight or almost so (Fig. 45). *A. minnamurrae*
- CuA + 1A distinctly bent anteriorly, with or without appendix at bend (e.g. Fig. 50). 7
7. Western Australian species (Figs 2–6). *A. australis*
- Eastern Australian species. 8
8. Male. 9
- Female. 20
9. Tergite 9 with lateral process on each side (e.g. Fig. 13). 10
- Tergite 9 without lateral process (e.g. Fig. 8). 14
10. Dististyles curved evenly throughout (e.g. Fig. 68). 11
- Dististyles bowed strongly at about midlength, basal and apical third almost straight (e.g. Fig. 31). 13

11. Median lobe of tergite 9 (portion between lateral processes) longer than wide, lateral processes opposing each other below median lobe (Fig. 68). *A. spinosa*
 —Median lobe of tergite 9 much wider than long, lateral processes not opposing each other (e.g. Fig. 13). 12
12. Lateral processes of tergite 9 long and horn-like (Fig. 13). *A. capricornis*
 —Lateral processes of tergite 9 short and subtriangular (Fig. 87). *A. victoriae*
13. Lateral processes of tergite 9 long and horn-like (Fig. 51). *A. similis*
 —Lateral processes of tergite 9 short and subtriangular (Fig. 31). *A. denticulata*
14. Dististyles bent strongly at about $\frac{2}{3}$ length, basal and apical portion almost straight (Fig. 39). *A. macalpinei*
 —Dististyles curved evenly throughout (e.g. Fig. 56). 15
15. Dististyles tapering evenly throughout (e.g. Fig. 56). 16
 —Dististyles almost parallel-sided for about basal $\frac{2}{3}$ of length, thence tapering irregularly (e.g. Fig. 23). 19
16. Parameres forming a trifid structure (e.g. Fig. 56). *A. simplex*
 —Parameres forming a simple slender cone of variable shape. 17
17. Tergite 9 very short, with posterior margin widely and evenly rounded; parameres not longer than aedeagus (in ventral aspect) (Fig. 8). *A. barrydayi*
 —Tergite 9 of variable but moderate length, with posterior margin not widely and evenly rounded; parameres markedly longer than aedeagus (in ventral aspect) (e.g. Fig. 62). 18
18. Posterior margin of tergite 9 with narrow U-shaped median excision (Figs 62, 64). *A. sinuosa*
 —Posterior margin of tergite 9 without narrow U-shaped median excision (Fig. 93). *A. zentae*
19. Parameres more than twice as long as aedeagus (in ventral aspect) (Fig. 78). *A. tonnoiri*
 —Parameres only slightly longer than aedeagus (in ventral aspect) (Fig. 23). *A. commoni*
20. Posterior portion of sternite 8 appearing in ventral aspect at least as long as half its width (e.g. Fig. 34). 21
 —Posterior portion of sternite 8 appearing in ventral aspect not longer than half its width (e.g. Fig. 29). 25
21. Posterior portion of sternite 8 appearing in ventral aspect considerably wider at base than at level of median notch (e.g. Fig. 34). 22
 —Posterior portion of sternite 8 appearing in ventral aspect not much wider at base than at level of median notch (e.g. Fig. 16). 24
22. Sternite 8 with distinct mediobasal protrusion (e.g. Figs 33, 34). 23
 —Sternite 8 without distinct mediobasal protrusion (Figs 53, 54). *A. similis*
23. Protrusion of sternite 8 substantial and widely rounded (Figs 33, 34). *A. denticulata*
 —Protrusion of sternite 8 a small and narrow cone (Figs 70, 71). *A. spinosa*
24. Median notch of sternite 8 shallower than half length of posterior portion of sternite (Fig. 16). *A. capricornis*

- Median notch of sternite 8 deeper than half length of posterior portion of sternite (Fig. 91). *A. victoriae*
- 25. Sternite 7 very short, W-shaped from ventral aspect, a cone-shaped lateral sclerite each side (Fig. 29). *A. commoni*
- Sternite 7 not very short or W-shaped from ventral aspect, no cone-shaped lateral sclerite (e.g. Fig. 60). 26
- 26. Lobes of sternite 8 very wide, short and evenly rounded and separated by very shallow notch (Fig. 81). *A. tonnoiri*
- Lobes of sternite 8 not very wide, short and evenly rounded, notch between them not very shallow (e.g. Fig. 11). 27
- 27. Sternite 8 with distinct mediobasal protrusion (e.g. Figs 10, 11). 28
- Sternite 8 only slightly arched mediobasally (e.g. Figs 59, 60). 29
- 28. Sternite 8 with sharp nose-like mediobasal protrusion (Figs 43, 44). *A. macalpinei*
- Sternite 8 with rounded mediobasal protrusion (Figs 10, 11). *A. barrydayi*
- 29. Tergite 9 not longer than tergite 7 (Figs 59, 60). *A. simplex*
- Tergite 9 longer than tergite 7 (e.g. Fig. 66). 30
- 30. Posterior portion of sternite 8 about as long as basal portion, median notch V-shaped (Fig. 66). *A. sinuosa*
- Posterior portion of sternite 8 much shorter than basal portion, median notch U-shaped (Fig. 96). *A. zentae*
- 31. Male. 32
- Female (not known for *N. collessi*). 34
- 32. Basistyles with substantial spine-like process (Figs 109, 110). *N. farecta*
- Basistyles without spine-like process (e.g. Figs 99, 100). 33
- 33. Tergite 9 posteromedially excised (Fig. 98). *N. bickeli*
- Tergite 9 posteromedially not excised (Fig. 104). *N. collessi*
- 34. Sternite 8 with median notch as deep as length of sternite in midline (Fig. 102). *N. bickeli*
- Sternite 8 with median notch not as deep as length of sternite in midline (Fig. 112). *N. farecta*

Genus *Austrothaumalea* Tonnoir

Austrothaumalea Tonnoir, 1927: 109. Type species
Austrothaumalea neozealandica Tonnoir.

Redescription. Mesothorax without any sign of antealar ridges. Abdomen with tergites 1–9, sternites 1–7 and ventral bridge of tergite 9 (=sternite 9) well developed in male; sternite 8 absent. Tergites and sternites 1–9 developed in female. Head, thorax, legs and abdomen covered with bristles of variable size; largest bristles along eye margin, in front of and between wing bases, on scutellum and on all abdominal sclerites.

Wing: broad with tip broadly rounded; macrotrichia present generally on C, wing margin and R_{1+2} ,

exceptionally in addition on R_{4+5} , never on membrane; C weakened and flexed (slightly concave) at about level of crossvein m-cu. Sc short and weak, running very close and parallel to R for a short distance and flexed perpendicularly into it slightly proximally to crossvein m-cu; humeral crossvein slightly distal to level of proximal side of basal cells; both Sc and humeral crossvein sometimes very faint or obsolete; R_{1+2} ending well beyond middle of wing, strongly flexed into first basal cell and seemingly dividing it in two; this cell not, however, divided by the vein itself, but by a slightly sclerotized area adjacent to it, which apparently functions as a hinge when wing is bent. R_3 usually more or less sinuous, more rarely just arched posteriorly; the

transverse R_2 generally markedly closer to the end of R_{1+2} than to the origin of R_{2+3} ; R_{4+5} and M_{1+2} very slightly arched posteriorly; M_{3+4} more or less sinuous, its base much shorter than crossvein m-cu; CuA + 1A generally angulated and bent or distinctly bowed anteriorly somewhat distal to crossvein m-cu, rarely almost straight; frequently a short appendix (incomplete base of 1A) directed posteroproximally at this bend.

Male genitalia: tergite 9 moderately wide and of very variable length, with well developed ventral bridge (= sternite 9); basistyles of variable length and shape,

attached by membrane to ventral bridge of tergite 9; parameres fused medially to form a slender, straight, arched or sinuous structure with simple, bifid or trifid apex; aedeagus generally well developed and of very variable shape.

Female genitalia: sternite 7 variable, but rarely strongly modified; sternite 8 highly modified, bilobed; sternite 9 strongly modified, heavily sclerotized but generally largely covered by lobes of sternite 8; tergite 9 of variable length, posterolateral corner never produced.

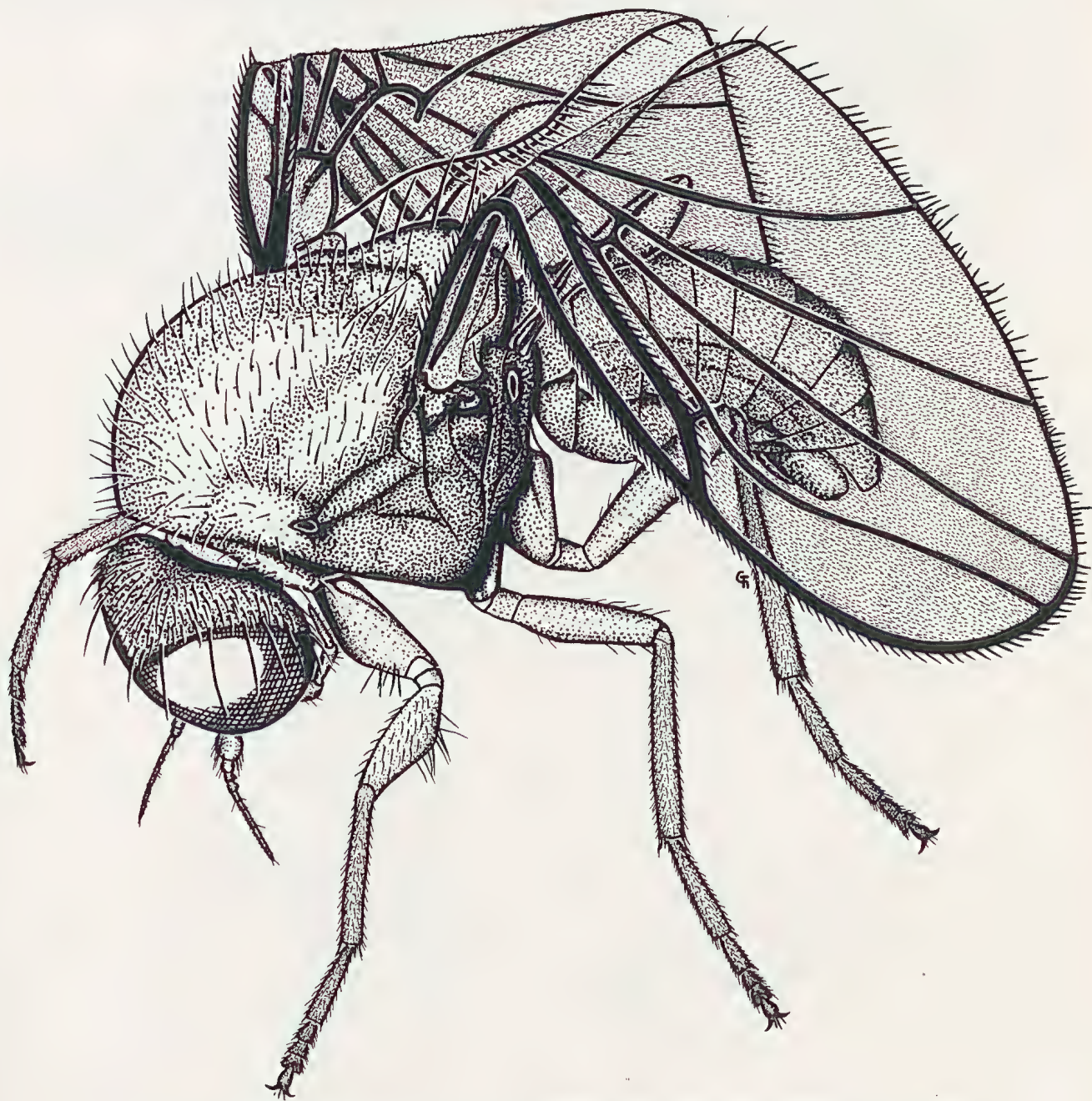


Fig. 1. *Austrothaumalea cervulus*, male, wings characteristically folded, drooping over the sides of the body. Scale = 1.0 mm.

Austrothaumalea australis n. sp.

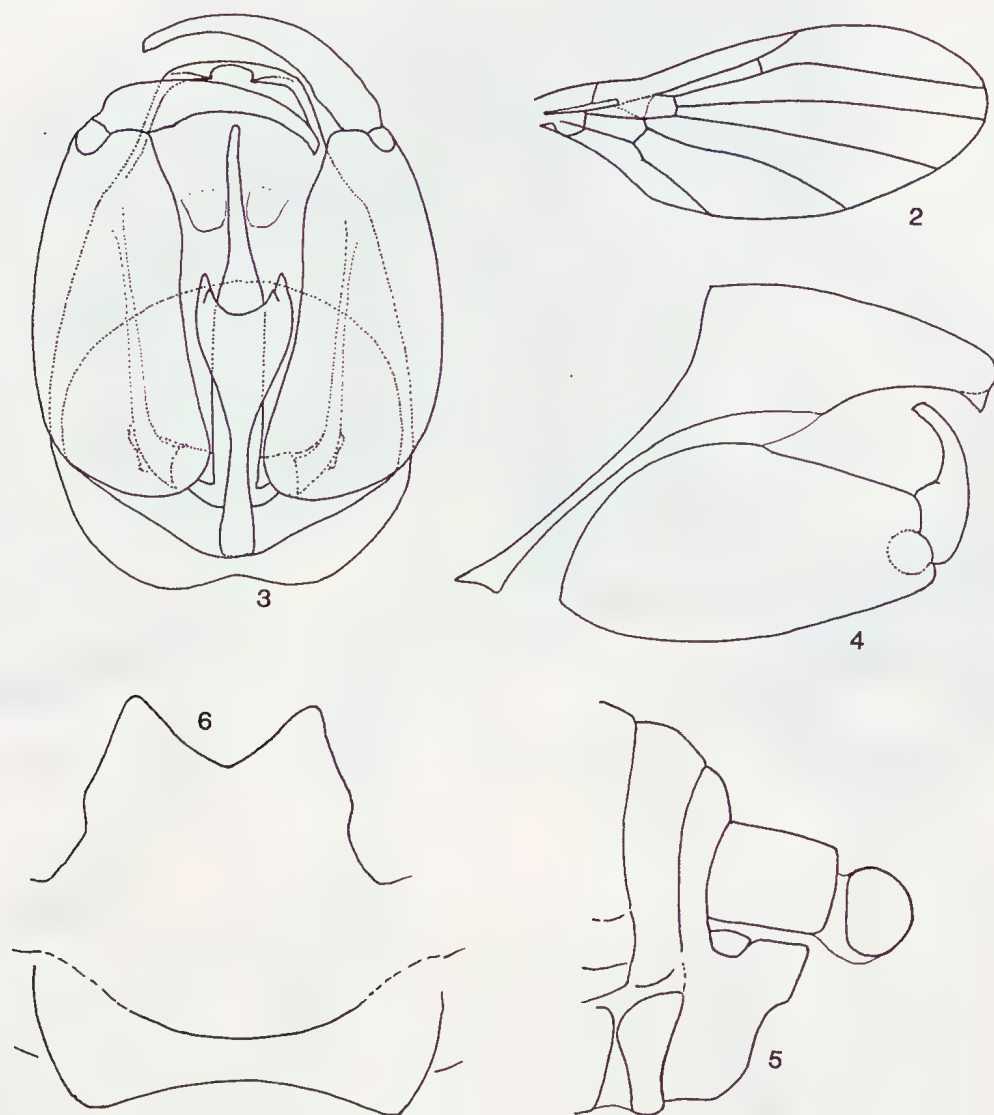
Figs 2-6

Material examined. HOLOTYPE ♂: Western Australia, 4.8 km north-east of Pimelia, nr Pemberton, 5 Oct 1970, D.H. Colless (ANIC). PARATYPES: Western Australia, all collected by D.H. Colless (ANIC): 4 ♂, 3 ♀, same data as holotype; 3 ♂, 2 ♀, Channybearup, nr Pemberton, 5 Oct 1970; 2 ♂, 1 ♀, Mount Chudalup, south of Northcliffe, 6 Oct 1970; 2 ♂, 3.2 km west of Karridale, 3 Oct 1970; 1 ♀, Nornalup, 9 Oct 1970; 1 ♀, Pemberton, 6 Oct 1970; 1 ♂, 1 ♀, 11.3 km north-east of Pemberton, 5 Oct 1970; 1 ♂, 2 ♀, Porongurup National Park, 11 Oct 1970; 1 ♂, 2 ♀, 9.7 km north of Walpole, 7 Oct 1970.

Description. Colouration: head dark brownish grey; thorax dull brownish yellow to dark ochreous; coxae, trochanters and femora pale to dull yellow, remaining leg segments brown; wing and haltere greyish yellow; abdomen pale greyish to blackish brown.

Wing: R_3 very slightly sinuous; CuA + 1A distinctly bent, with or without very slight indication of an appendix.

Male genitalia: tergite 9 long, narrow, trapezoid, with posterior margin slightly convex, with one apical, ventrally directed triangular tooth on each side; basistyles not reaching posterior margin of tergite 9; dististyles not long, slightly and evenly curved and



Figs 2-6. *Austrothaumalea australis* n. sp. 2-4, male: 2, wing; 3,4, genitalia: 3, ventral; 4, lateral. 5,6, female: 5, genitalia, lateral; 6, sternites 7 and 8.

tapering throughout length, with blunt tips; parameres forming a wide-based but otherwise moderately long, narrow and slightly dorsally curved cone; aedeagus appearing tulip-shaped from ventral aspect.

Female genitalia: tergite 9 much longer than either tergite 7 or 8; sternite 7 very short in midline; sternite 8 sinuous from lateral aspect, with very wide V-shaped notch between substantial subtriangular lobes.

Dimensions: wing length, ♂ 2.0–2.2 mm, ♀ 2.2–2.7 mm.

Distribution. South-western Australia.

Etymology. The specific name is the Latin adjective *australis* (=southern), referring to the distribution of this species.

Austrothaumalea barrydayi n. sp.

Figs 7–11

Material examined. HOLOTYPE ♂: New South Wales, Mooney Mooney Creek, nr Gosford, 12 Dec 1978, D.K. McAlpine & B.J. Day (AM). PARATYPES: New South Wales: 2 ♀, Macquarie Falls, 1 & 14 Nov 1960, D.H. Colless (ANIC); 2 ♀, Mooney Mooney Creek, nr Gosford, 23 Nov 1956 & 9 Nov 1957, D.K. McAlpine (AM); 1 ♀, Mount Kembla, 12

Feb 1932, A. Tonnoir (ANIC); 2 ♀, Royal National Park, 3 & 23 Nov 1956, D.K. McAlpine (AM).

Description. Colouration: head dark brownish grey; thorax pale brownish yellow, pleura largely somewhat darker than the rest; legs yellowish brown to dark greyish brown; wing and haltere yellowish to pale greyish brown; abdomen greyish brown.

Wings: R_3 very strongly sinuous; CuA + 1A distinctly bent, with indication of an appendix.

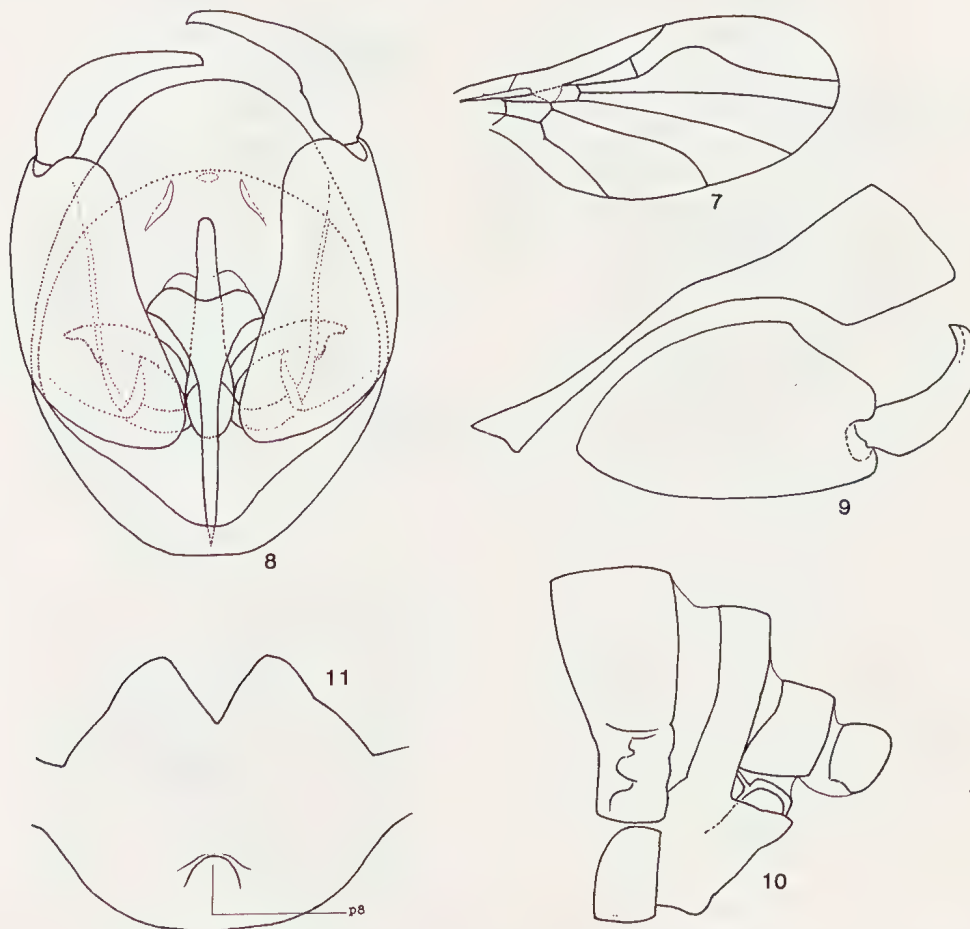
Male genitalia: tergite 9 short, almost semicircular from dorsal aspect; basistyles not reaching posterior margin of tergite 9; dististyles slender, curving and tapering evenly from a moderately wide base into a weakly hooked apex; parameres forming a slender short cone which appears cut off apically; aedeagus with base long and narrow, and apex wide and wing-like.

Female genitalia: tergite 9 longer than tergite 8 but shorter than tergite 7; sternite 8 with mediobasal rounded swelling, notch V-shaped, lobes wide, subtriangular.

Dimensions: wing length, ♂ 1.9–2.0, ♀ 2.2–2.4 mm.

Distribution. New South Wales.

Etymology. This species is dedicated to Mr Barry Day, one of its collectors.



Figs 7–11. *Austrothaumalea barrydayi* n. sp. 7–9, male: 7, wing; 8, 9, genitalia: 8, ventral; 9, lateral. 10, 11, female: 10, genitalia, lateral; 11, sternite 8. p8, protrusion of sternite 8.

Austrothaumalea capricornis n. sp.

Figs 12–16

Material examined. HOLOTYPE ♂: New South Wales, Blue Mountains, Mount Wilson, 3 May 1958, D.K. McAlpine (AM). PARATYPES: New South Wales: 1 ♀, same data as holotype (AM); 1 ♂, Point Lookout nr Ebor, 1524 m, 21 Mar 1960, D.K. McAlpine (AM); 1 ♂, Point Lookout, New England National Park, 30°29'S, 152°25'E, 12–22 Feb 1984, I.D. Naumann (ANIC); 2 ♀, Toms Cabin, New England National Park, 30°30'S, 152°24'E, 12–22 Feb 1984, I.D. Naumann (ANIC).

Description. Colouration: head dark grey; thorax dark brownish yellow; legs dull yellowish to greyish brown; wing and haltere pale yellowish to greyish brown; abdomen greyish brown.

Wing: R₃ sinuous; CuA+1A distinctly bent and with clear indication of an appendix.

Male genitalia: tergite 9 wide, trapezoid, with ventrolateral posteriorly directed, straight or slightly undulate horn-like process each side; basistyles reaching almost posterior margin of tergite 9; dististyles slim, curving and tapering evenly throughout, with blunt apex; parameres forming a very long narrow pointed

cone; aedeagus Y-shaped, with stem long, branches short and bearing several teeth of different length apically.

Female genitalia: tergite 9 markedly longer than tergite 8; sternite 8 strongly bent dorsally near base as seen from lateral aspect; a V-shaped notch between subtriangular lobes.

Dimensions: wing length, ♂ 2.0–2.2 mm, ♀ 2.1–2.3 mm.

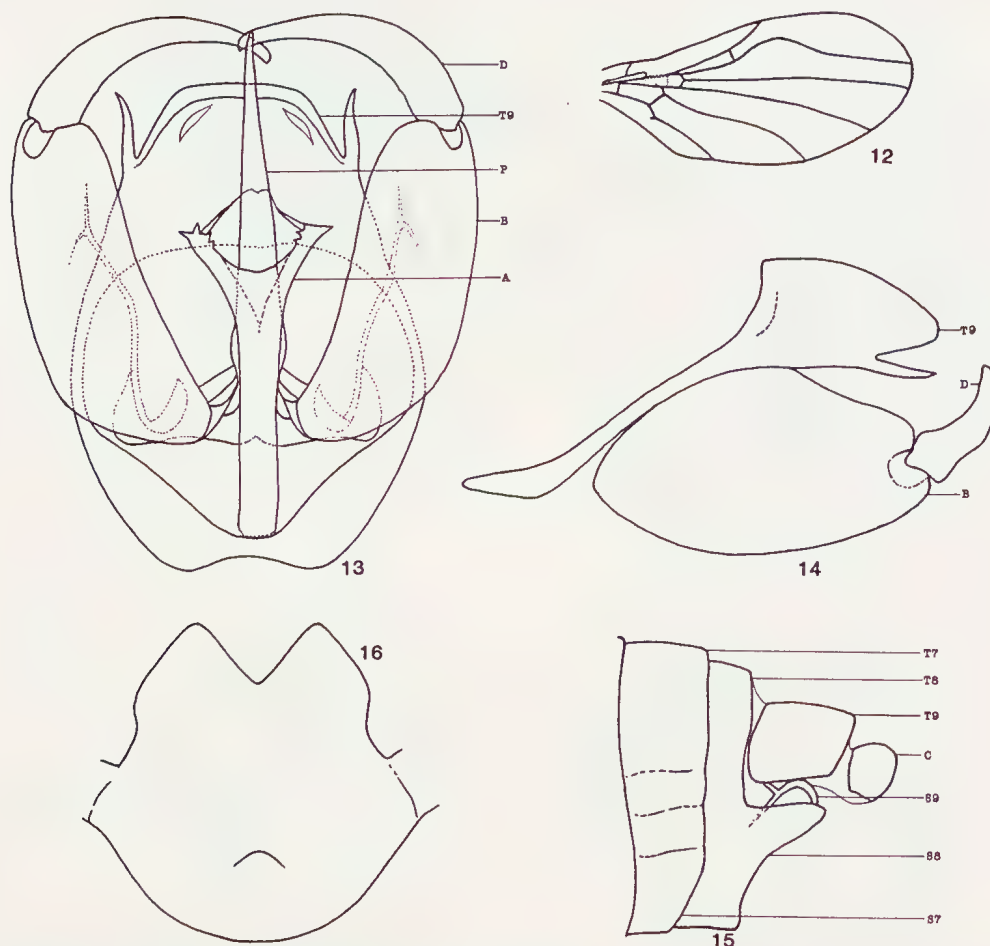
Distribution. New South Wales.

Etymology. The specific name is a Latin adjective referring to the processes on tergite 9 of the male of this species, which resemble the horns of a goat.

Austrothaumalea cervulus n. sp.

Figs 17–22

Material examined. HOLOTYPE ♂: New South Wales, Fitzroy Falls, 3 Oct 1938, A.L. Tonnoir (ANIC). PARATYPES: New South Wales: 1 ♀, Belmore Falls, 23 Jan 1963, D.H. Colless (ANIC); 1 ♀, Waterfall, Royal National Park, 29 Dec 1961, D.H. Colless (ANIC); 2 ♂, 1 ♀, Waterfall, National Falls, 2 Oct 1985, G. Theischinger & A. Neboiss (GT).



Figs 12–16. *Austrothaumalea capricornis* n. sp. 12–14, male: 12, wing; 13, 14, genitalia: 13, ventral; 14, lateral. 15, 16, female: 15, genitalia, lateral; 16, sternite 8. A, aedeagus; B, basistyle; C, cercus; D, dististyle; S, sternite; T, tergite.

Additional material. 1 specimen (abdomen missing), New South Wales, Audley, Royal National Park, 14 Nov 1960, D.H. Colless (ANIC).

Description. Colouration: head and thorax blackish brown; coxae, trochanters and femora brownish yellow, remaining leg segments yellowish to blackish brown; wing and haltere greyish brown; abdomen greyish brown.

Wing: R_3 very slightly sinuous; CuA + 1A distinctly bent and with substantial appendix.

Male genitalia: tergite 9 wide, trapezoid with posterior corners slightly rounded; basistyles reaching far short of posterior margin of tergite 9; dististyles forked, with wide cylindrical base, wider straight conical outer

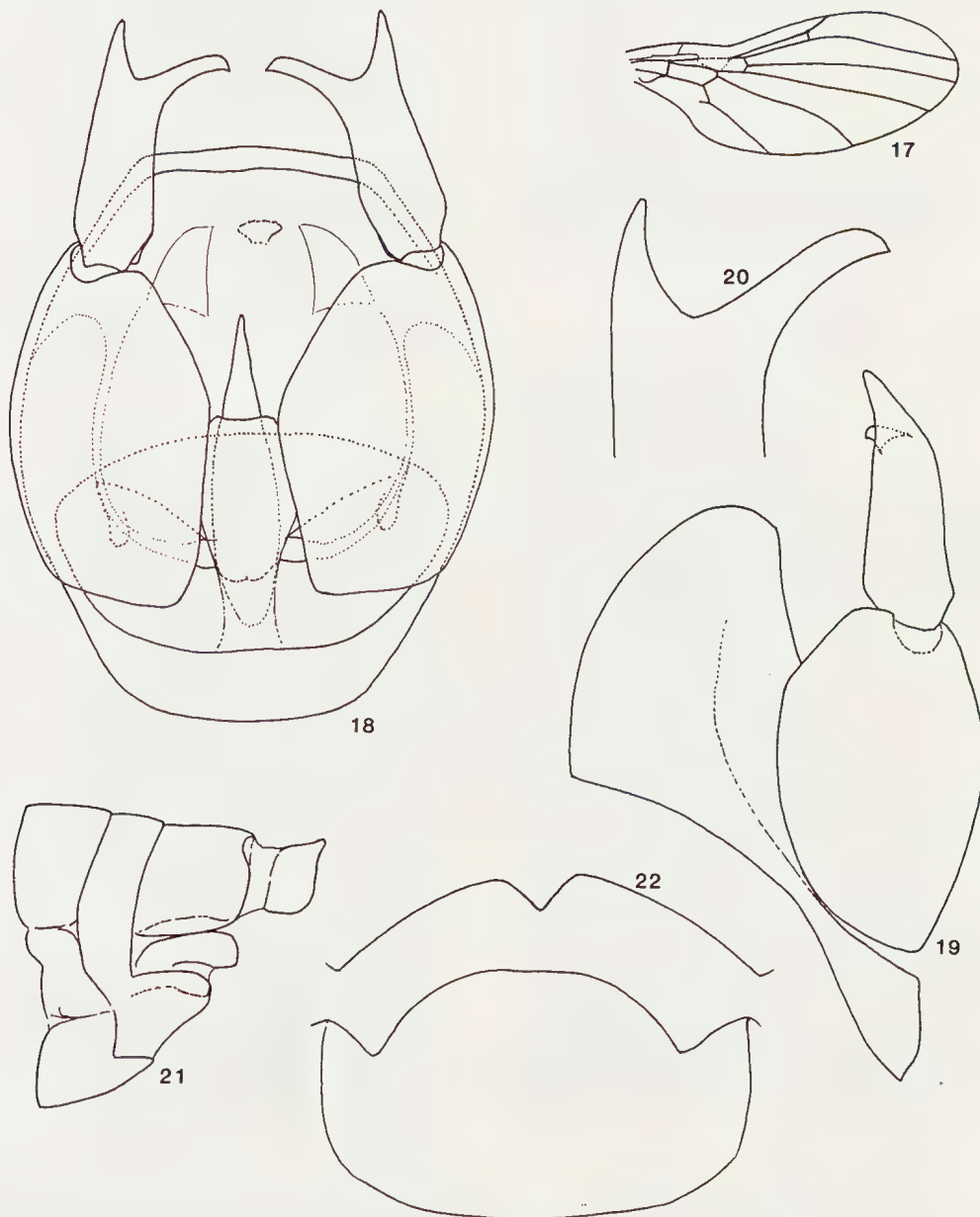
branch and narrower cylindrical, apically weakly hooked, inner branch; parameres forming a short narrow cone; aedeagus appearing broadly spoon-shaped from ventral aspect.

Female genitalia: tergite 9 longer than either tergite 7 or 8; sternite 7 produced medially into a wide lobe; sternite 8 with shallow V-shaped notch between very short and wide lobes; cerci with posterodorsal corner produced.

Dimensions: wing length, ♂ 1.8–1.9 mm, ♀ 2.1–2.2 mm.

Distribution. New South Wales.

Etymology. The specific name *cervulus* (Latin: small deer) refers to the antler-like dististyles of this species.



Figs 17–22. *Austrothaumalea cervulus* n. sp. 17–20, male: 17, wing; 18, 19, genitalia; 18, ventral; 19, lateral; 20, apical portion of dististyle. 21, 22 female: 21, genitalia, lateral; 22, sternites 7 and 8.

Austrothaumalea comuni n. sp.

Figs 23-29

Material examined. HOLOTYPE ♂: New South Wales, Clyde Mountain, 732 m, 21 Mar 1961, I.F.B. Common & M.S. Upton (ANIC). PARATYPES: New South Wales: 1 ♀, Fitzroy Falls, 3 Oct 1938, A.L. Tonnoir (ANIC); 1 ♀, Kangaroo Valley, 23 Mar 1961, D.H. Colless (ANIC); 1 ♀, Brown Mt., 25 Feb 1929, A.L. Tonnoir (ANIC).

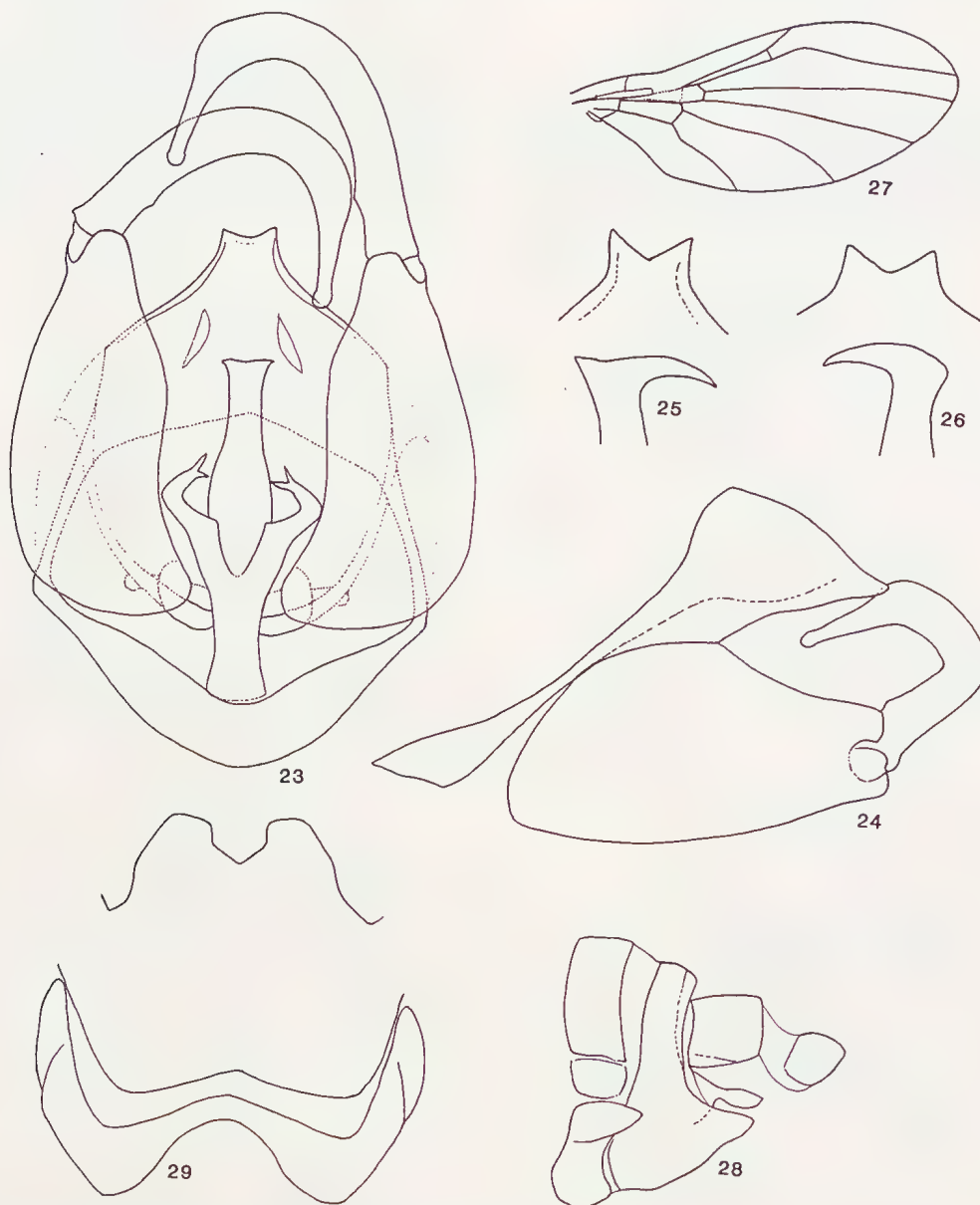
Additional material. New South Wales: 1 ♂, Lee's Spring, ACT, 13 Nov 1938, A.L. Tonnoir (ANIC); 1 ♂, Pretty Point Creek, Mt Kosciusko, 1670 m, 10 Dec 1931, A.L. Tonnoir (ANIC).

Description. Colouration: head dark grey; thorax yellowish brown; coxae, trochanters and femora pale

yellow, remaining leg segments yellow to yellowish brown; wing and haltere largely greyish yellow, a conspicuous but not sharply defined dark grey patch from about level of fork of R_{1+2} and R_3 to slightly beyond ending of R_{1+2} , and from C to M_{1+2} ; abdomen greyish brown.

Wings: R_3 slightly sinuous; CuA + 1A slightly bent, without any indication of an appendix.

Male genitalia: tergite 9 strongly and narrowly produced medially to end in 2 short subtriangular processes; basistyles reaching about as far as apical processes of tergite 9; dististyles long, slender, strongly but evenly curved, of about the same thickness from base to $\frac{1}{2}$ length, thence strongly tapering into a narrow, apically somewhat globular tip; parameres forming a



Figs 23-29. *Austrothaumalea comuni* n. sp. 23-26, male: 23, 24, genitalia of holotype: 23, ventral; 24, lateral; 25, 26, tip of tergite 9 and of parameres, ventral: 25, specimen from Lee's Spring, ACT; 26, specimen from Pretty Point Creek, Mt Kosciusko, NSW. 27-29, female: 27, wing; 28, genitalia, lateral; 29, sternites 7 and 8.

slender symmetrical vase-like structure in the holotype, an asymmetrical hook in the other specimens (see below); aedeagus appearing as a wide Y with the arms bent slightly outwards at first then strongly medially, each with 2 finger-like apical processes.

Female genitalia: tergite 9 about as long as tergites 7 and 8 together; sternite 7 very short along midline, W-shaped from ventral aspect, with conical lateral process; sternite 8 with U-shaped notch between narrow, somewhat inwardly directed lobes.

Dimensions: wing length, ♂ unknown (wings of holotype largely destroyed), ♀ 2.2–2.3 mm.

Distribution. New South Wales.

Remarks. The wings of the holotype ♂ are largely destroyed. On the basis of the pattern of the remaining fractions of the male wings, two females from the same general area have been associated with the male. The description of the wing above is given from those females. Two males from different localities deviate from the holotype by asymmetry of the parameres and by the lack of a particular wing pattern, but share the venational wing details with the supposed females. Those males are only provisionally included in *A. commoni* and listed, therefore, separated from the types. The female from Brown Mountain has unpatterned wings.

Etymology. The species is dedicated to Dr I.F.B. Common, one of its collectors.

Austrothaumalea denticulata n. sp.

Figs 30–34

Material examined. HOLOTYPE ♂: Tasmania, Hobart, 29 Oct 1933, A. Tonnoir (ANIC). PARATYPES: Queensland: 1 ♂, Ayr, 30 Sept 1960, R. Hughes (ANIC); 1 ♂, 1 ♀, Queen Mary Falls National Park, 3 Mar 1962, J.B. & M.M. (ANIC). New South Wales: 1 ♀, Barrington, 1–5 Feb 1925, SU Zoo Exp. (ANIC); 1 ♂, 2 ♀, Mongarlowe River, Clyde Mountain, 5 May 1965, D.H. Colless (ANIC); 2 ♂, 2 ♀, Rutherford Creek, Brown Mountain, 9 Aug 1962, Z.R. Liepa (ANIC); 2 ♂, Waterfall, National Falls, 2 Oct 1985, G. Theischinger & A. Neboiss (GT); 1 ♂, Mt Wilson, Blue Mountains, 12 Aug 1963, D.K. McAlpine (AM). Australian Capital Territory: 4 ♂, Mount Majura, Canberra, 22 & 25 Aug 1960, 1 ♂, same loc., 13 Sep 1960, 3 ♂, same loc., 29 Sept 1960, 1 ♂, same loc., 10 Apr 1961, 5 ♂, 1 ♀, same loc., 2 Apr 1963, D.H. Colless (ANIC); 1 ♂, 1 ♀, Mount Tidbinbilla, 29 Oct 1939, A.L. Tonnoir (ANIC). Victoria: 1 ♂, Alexandra, 27 May 1953, A. Neboiss (MV); 1 ♂, Grampians, 18 Oct 1967, N. Dobrotworsky (ANIC). Tasmania: 2 ♂, 5 ♀, Eaglehawk Neck, 15 & 22 Nov 1922, A. Tonnoir (ANIC); 1 ♂, Hobart, 3 Jan 1923, A. Tonnoir (ANIC); 7 ♂, 4 ♀, same data as holotype (ANIC); 1 ♀, Launceston, 25 Oct 1922, 2 ♂, 1 ♀, same loc., 17 Nov 1923, A. Tonnoir (ANIC); 1 ♂, 2 ♀, National Park, 15 & 17 Dec. 1922, A. Tonnoir (ANIC).

Description. Colouration: head dark brownish grey; thorax yellowish to medium brown; legs dull yellow to yellowish brown; wing and haltere yellowish to greyish brown; abdomen dull yellowish to dark brownish grey.

Wing: R_3 slightly sinuous; $CuA + 1A$ distinctly bent

and with distinct but short appendix.

Male genitalia: tergite 9 with evenly rounded, often almost semicircular, terminal median lobe flanked by a short triangular tooth each side, this tooth not bent downwards; basistyles reaching almost as far as lateral teeth of tergite 9; dististyles long, bowed strongly just before half length, basal portion somewhat more strongly tapered than apical portion, tip blunt; parameres forming a long narrow structure which appears hastate from ventral aspect and slightly arched from lateral aspect; aedeagus with long narrow base and slightly bifurcate apex.

Female genitalia: tergite 9 longer than either tergite 7 or 8; sternite 8 with substantial, widely rounded mediobasal protrusion, lobes subtriangular, apically rounded, median notch somewhat variable, U-V-shaped.

Dimensions: wing length, ♂ 2.2–2.7 mm, ♀ 2.6–3.5 mm.

Distribution. Queensland, New South Wales, Victoria and Tasmania.

Etymology. The specific name is from the Latin adjective *denticulatus* (= with small teeth), referring to the shape of tergite 9 of the male.

Austrothaumalea fusca n. sp.

Figs 35–38

Material examined. HOLOTYPE ♂: Tasmania, King River, 4 Feb 1923, A. Tonnoir (ANIC). PARATYPE: 1 ♂, same data as holotype (ANIC).

Description (male). Colouration: head greyish brown; thorax dull greyish brown; coxae, trochanters and femora yellowish, remaining leg segments brownish yellow to dark brown; wing and haltere grey; abdomen greyish brown.

Wing: R_3 not sinuous; $CuA + 1A$ distinctly bent and with well developed appendix.

Genitalia: tergite 9 trapezoid, with rounded corners and emarginate posterior margin, without lobes or teeth; basistyles short and wide, reaching far short of posterior margin of tergite 9; dististyles short, slightly bowed at about half length, basal half hardly tapering, apical half strongly tapering; parameres forming a basally wide, conical structure with narrow apex; aedeagus very weakly sclerotized and hardly discernible, wide basally, otherwise tulip-shaped from ventral aspect.

Dimensions: wing length 2.2–2.3 mm.

Distribution. Tasmania.

Etymology. The specific name is from the Latin adjective *fuscus* (= dark), referring to the dark wings of this species.

Austrothaumalea macalpinei n. sp.

Figs 39–44

Material examined. HOLOTYPE ♂: New South Wales, Otford, 7 Oct 1961, D.K. McAlpine (AM). PARATYPES: New

South Wales: 1 ♀, same data as holotype (AM); 1 ♂, Kangaroo Valley, 23 Mar 1961, D.H. Colless (ANIC); 1 ♀, Otford, Royal National Park, 31 Dec 1962, D.H. Colless (ANIC).

Description. Colouration: head dark yellowish to greyish brown; thorax dark yellowish brown; legs brownish yellow to greyish brown; wing and haltere rather dark greyish brown; abdomen greyish brown.

Wing: R_3 strongly sinuous; CuA + 1A distinctly bent and with small but distinct appendix.

Male genitalia: tergite 9 narrow, long, trapezoid, posterior margin produced ventrally to form cap-like apex; basistyles reaching far short of posterior margin of tergite 9; dististyles almost spheroid in basal third,

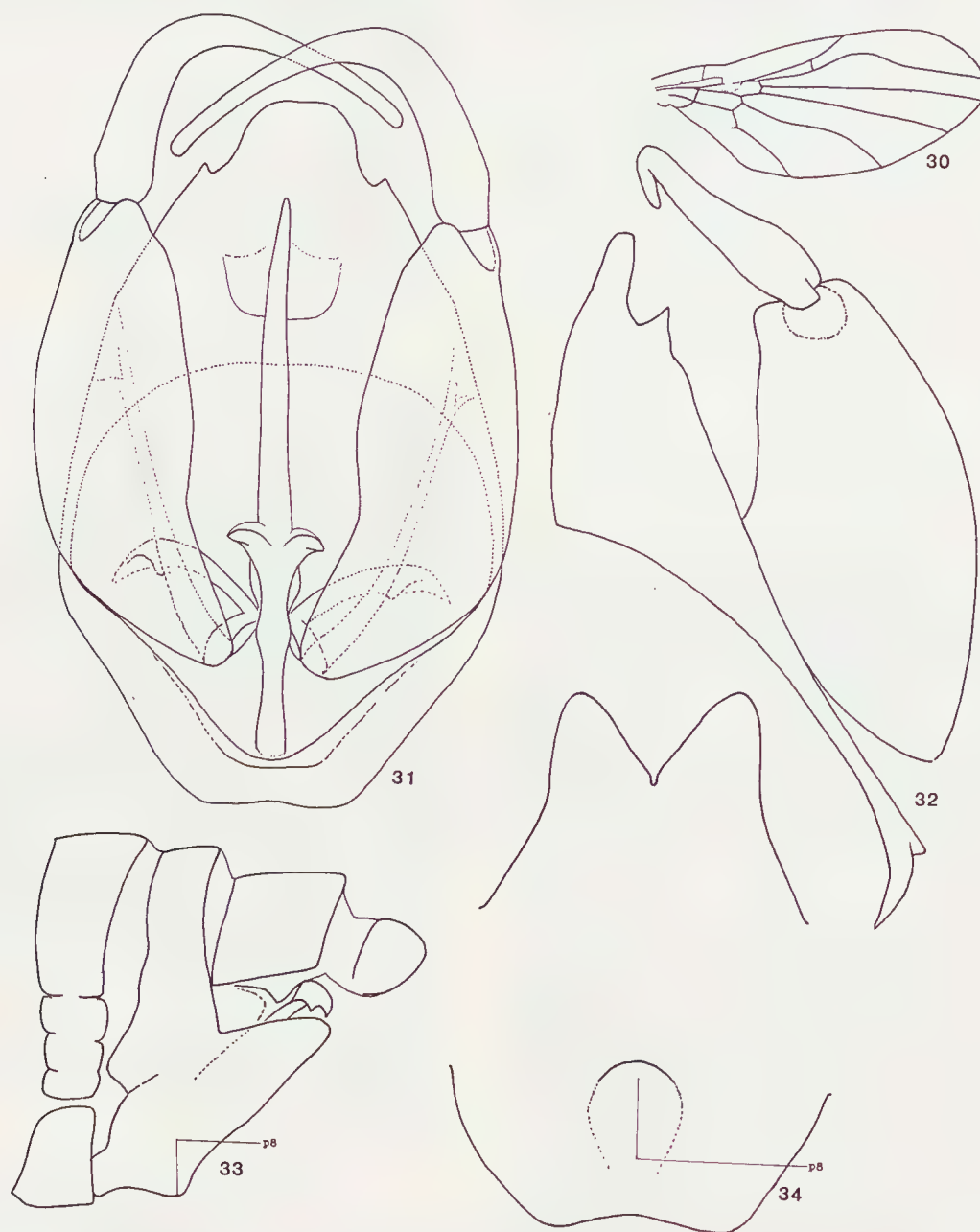
strongly bent at about two thirds length; parameres forming a long narrow slightly curved cone; aedeagus goblet-shaped in ventral aspect.

Female genitalia: tergite 9 slightly produced in midline, markedly longer than tergite 8; sternite 8 with narrow nose-like protrusion near base, a shallow notch between short and wide rounded lobes.

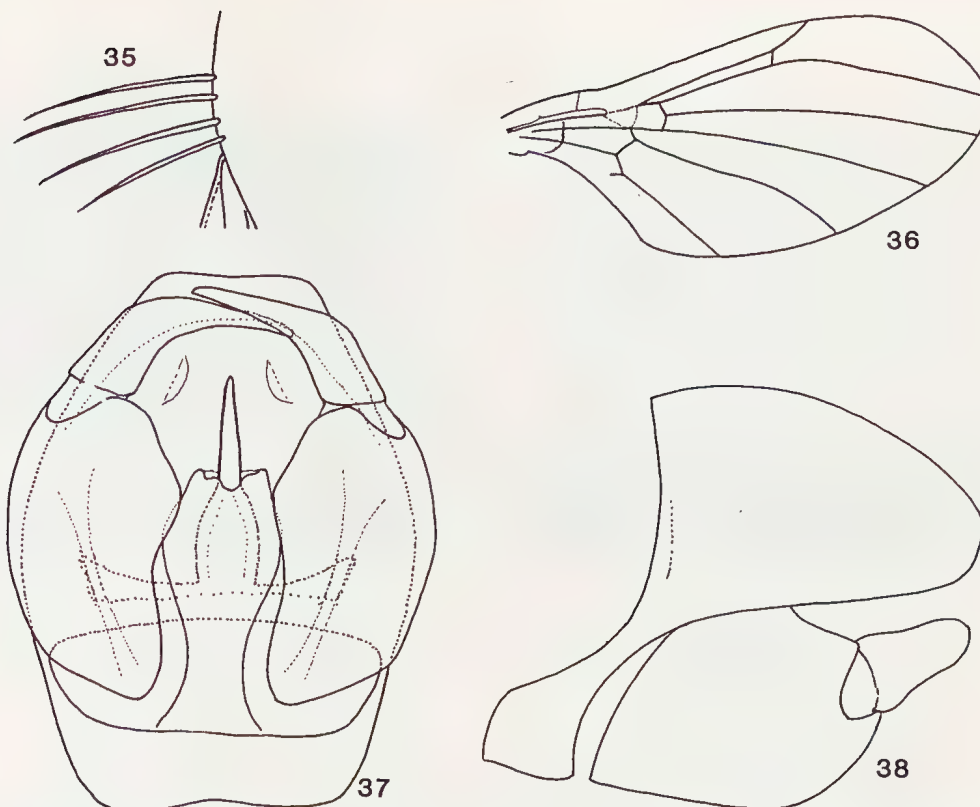
Dimensions: wing length, ♂ 1.9–2.0 mm, ♀ 2.3–2.5 mm.

Distribution. New South Wales.

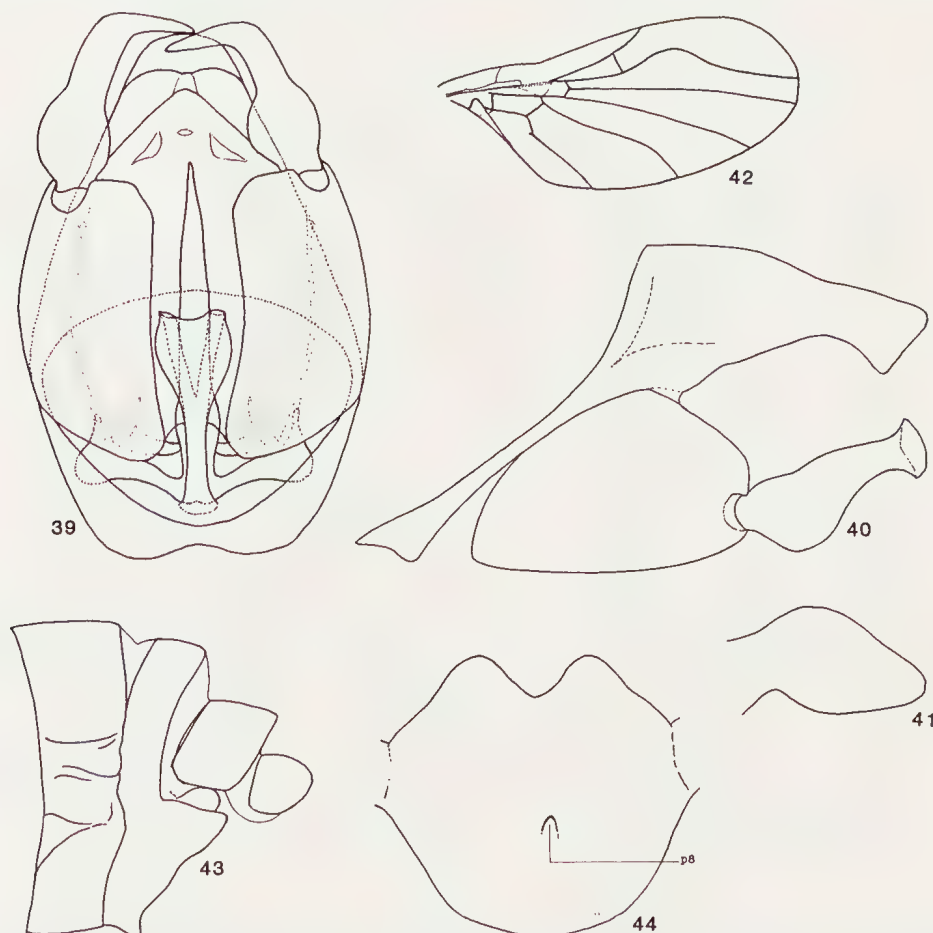
Etymology. This species is dedicated gratefully to Dr D.K. McAlpine, in recognition of the help he has given me.



Figs 30–34. *Austrothaumalea denticulata* n. sp. 30–32, male: 30, wing; 31, 32, genitalia: 31, ventral; 32, lateral. 33, 34, female: 33, genitalia, lateral; 34, sternite 8. p8, protrusion of sternite 8.



Figs 35–38. *Austrothaumalea fusca* n. sp., male. 35, left side of thorax and wing base, dorsal; 36, wing; 37, 38, genitalia: 37, ventral; 38, lateral.



Figs 39–44. *Austrothaumalea macalpinei* n. sp. 39–41, male: 39, 40, genitalia: 39, ventral; 40, lateral; 41, apical portion of dististyle, caudal. 42–44, female: 42, wing; 43, genitalia, lateral; 44, sternite 8. p8, protrusion of sternite 8.

Austrothaumalea minnamurrae n. sp.

Figs 45-49

Material examined. HOLOTYPE ♂: New South Wales, Minnamurra Falls, 16 Nov 1960, I.F.B. Common & M.S. Upton (ANIC). PARATYPES: New South Wales: 1 ♂, same data as holotype (ANIC); 4 ♂, Pretty Point Creek, Mt Kosciusko, 13 Dec 1931, A.L. Tonnoir (ANIC); 2 ♂, Waterfall, National Falls, 2 Oct 1985, G. Theischinger & A. Neboiss (GT).

Additional material. 1 ♂, Queensland, Woombye nr Nambour, 11-16 Oct 1965, D.H. Colless (ANIC).

Description (male). Colouration: head dark brown to blackish brown; thorax greyish brown to blackish brown; coxae, trochanters and femora yellowish brown, remaining leg segments yellowish brown to greyish

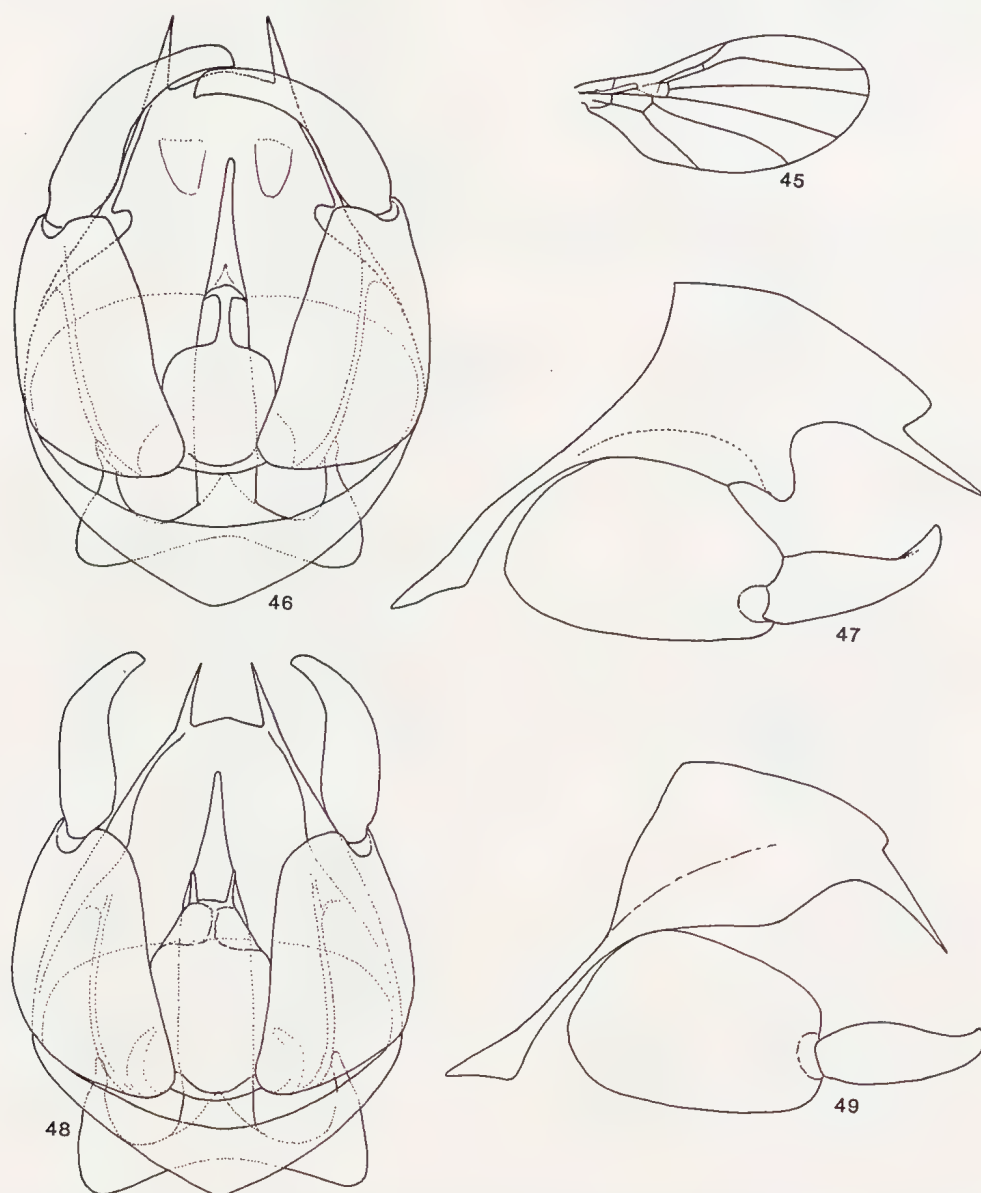
brown; wing and haltere greyish yellow to pale brownish grey; abdomen pale greyish brown.

Wing: R_3 very slightly sinuous; $CuA + 1A$ almost straight and without any sign of an appendix.

Genitalia: tergite 9 trapezoid with posterior margin convex and posterior corners very strongly produced to form long thin processes, ventrolateral corner produced but rounded; basistyles reaching only as far as ventrolateral corners of tergite 9; dististyles evenly curved, tapering evenly from a moderately wide base to a rather blunt apex; parameres forming a long thin cone; aedeagus basally wide, bell-shaped, as seen from ventral aspect.

Dimensions: wing length 1.5-1.7 mm.

Distribution. ?Queensland and New South Wales.



Figs 45-49. *Austrothaumalea minnamurrae* n. sp., male. 45, wing, specimen from Pretty Point Creek, Mt Kosciusko, NSW; 46, 47, genitalia, specimen from Minnamurra Falls, NSW; 46, ventral; 47, lateral; 48, 49, genitalia, specimen from Woombye, Qld; 48, ventral; 49, lateral.

Remarks. As can be seen from comparing Figs 46, 47 with 48, 49, the specimen from Queensland differs from the typical specimens by having less strongly produced ventrolateral corners of tergite 9, shorter dististyles and small processes on the aedeagus. It is, therefore, only provisionally included in *A. minnamurrae*.

Etymology. The specific name *minnamurrae* refers to the type locality (Minnamurra Falls) of this species.

Austrothaumalea similis n. sp.

Figs 50–54

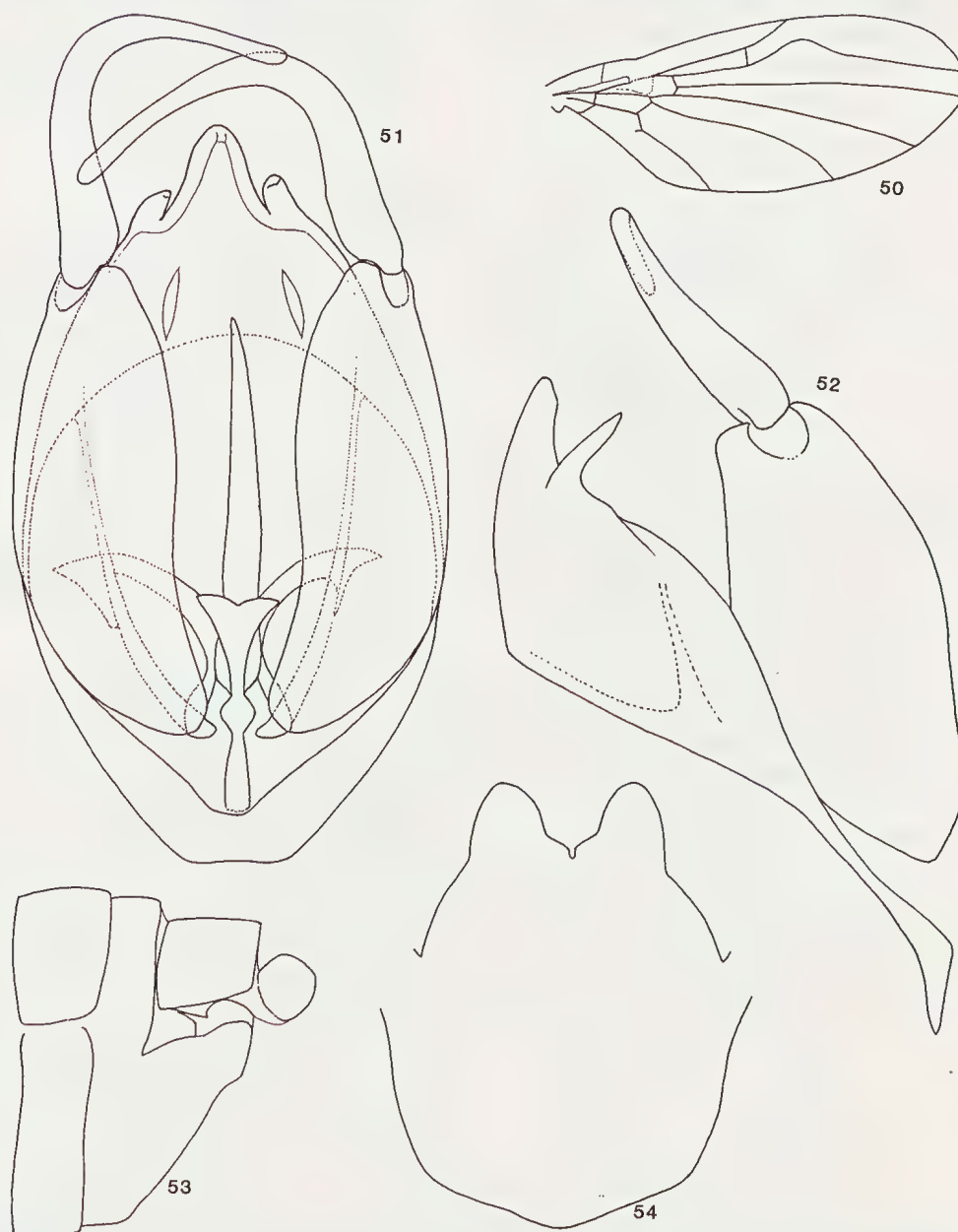
Material examined. HOLOTYPE ♂: Tasmania, Mount Hicks, 20 Oct 1933, A.L. Tonnoir (ANIC). PARATYPES:

Tasmania: 2 ♂, 5 ♀, same data as holotype (ANIC); 4 ♂, Burnie, 27 Oct 1922, 2 ♂, same loc., 21 Oct 1933, A. Tonnoir (ANIC).

Description. Colouration: head dark greyish brown; thorax brownish yellow; legs pale to greyish yellow; wing and haltere yellowish to greyish brown; abdomen yellowish to dark greyish brown.

Wing: R_3 sinuous; CuA+1A distinctly bent and with well developed appendix.

Male genitalia: tergite 9 produced medially into an elongate more or less rounded lobe flanked on each side by one sharp tooth, bent downwards at about a right angle; basistyles not reaching beyond level of lateral tooth of tergite 9; dististyles long, slender, strongly but evenly curved at about their middle, tapering nicely



Figs 50–54. *Austrothaumalea similis* n. sp. 50–52, male: 50, wing; 51,52, genitalia: 51, ventral; 52, lateral. 53,54, female: 53, genitalia, lateral; 54, sternite 8.

from a moderately wide base into a narrow blunt tip; parameres forming a single narrow, slightly dorsally curved stylet-shaped structure; aedeagus long and narrow, slightly thickened at about its middle, slightly swallow-tailed apically.

Female genitalia: tergite 9 longer than tergite 8; sternite 8 swollen mediobasally but without distinct protrusion, lobes apically rounded, median notch generally U-shaped.

Dimensions: wing length, ♂ 2.3–2.6 mm, ♀ 2.8–3.1 mm.

Distribution. Tasmania.

Etymology. The specific name is the Latin adjective

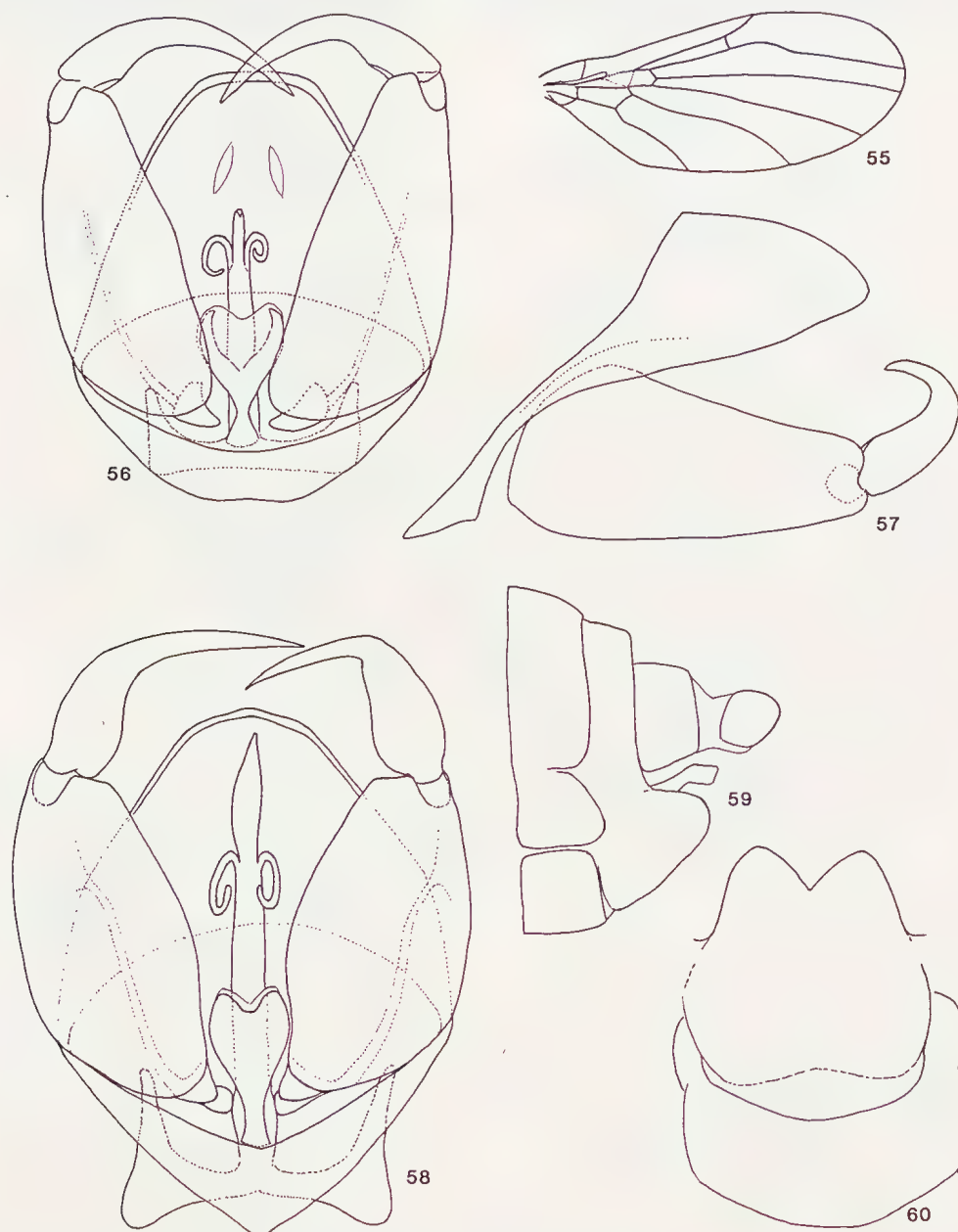
similis (= similar), referring to the similarity of this species to others, particularly *A. denticulata*.

Austrothaumalea simplex n. sp.

Figs 55–60

Material examined. HOLOTYPE ♂: Tasmania, Eaglehawk Neck, 18 Nov 1922, A. Tonnoir (ANIC). PARATYPES: Tasmania: 1 ♂, same data as holotype (ANIC); 1 ♀, Eaglehawk Neck, 22 Nov 1922, A. Tonnoir (ANIC); 1 ♂, Maria Island, 6 Nov 1933, A. Tonnoir (ANIC); 1 ♂, Weldboro Pass, 25 Oct 1933, A.L. Tonnoir (ANIC).

Additional material. 1 ♂, Tasmania, Mt Barrow, 945 m, 25 Jan 1960, D.K. McAlpine (AM).



Figs 55–60. *Austrothaumalea simplex* n. sp. 55–58, male: 55–57, specimen from Eaglehawk Neck, Tas.: 55, wing; 56, 57, genitalia: 56, ventral; 57, lateral; 58, specimen from Mt Barrow, Tas., genitalia, ventral. 59, 60, female: 59, genitalia, lateral; 60, sternites 7 and 8.

Description. Colouration: head dark grey; thorax yellowish to medium brown; legs yellowish to greyish brown; wing and haltere yellowish to brownish grey; abdomen pale to dark brownish grey.

Wing: R_3 slightly sinuous; $CuA + 1A$ distinctly bent but without any indication of an appendix.

Male genitalia: tergite 9 almost trapezoid with rounded corners, posterior margin almost straight, no distinct lateral corner and no teeth; basistyles reaching as far as posterior margin of tergite 9; dististyles slightly and evenly curved, gradually tapering from a moderately wide base into a rather narrow apex; parameres forming a structure with narrow stalk-like base and trifurcate apex, the lateral prongs bent anteroventrally; aedeagus Y-shaped, with short base.

Female genitalia: tergite 9 not longer than tergite 8; sternite 8 appearing almost straight from lateral aspect, a wide V-shaped notch between short subtriangular, apically rounded lobes.

Dimensions: wing length, ♂ 2.3–2.6 mm, ♀ 2.6 mm.

Distribution. Tasmania.

Remarks. As comparison between Figs 56 and 58 shows, the specimen from Mt Barrow has thicker basistyles, stronger bent dististyles and a thicker median branch of the parameres than typical males. It is, therefore, only provisionally included in *A. simplex*.

Etymology. The specific name is the Latin adjective *simplex* (=simple), referring to the shape of tergite 9 of the male and the female genitalia in this species.

Austrothaumalea sinuosa n. sp.

Figs 61–66

Material examined. HOLOTYPE ♂: New South Wales, Pretty Point Creek, Mt Kosciusko, 13 Dec 1931, A.L. Tonnoir (ANIC). PARATYPES: 4 ♂, 1 ♀, same data as holotype (ANIC).

Description. Colouration: head dark greyish brown; thorax dark yellowish to medium brown; legs dark yellowish to greyish brown; wing and haltere yellowish to greyish brown; abdomen greyish brown.

Wing: R_3 slightly sinuous; $CuA + 1A$ distinctly bent, with or without very slight indication of an appendix.

Male genitalia: tergite 9 trapezoid with posterior corners widely rounded from dorsal aspect; posterior margin strongly produced ventrally, with a U-shaped median excision; basistyles reaching posterior margin of tergite 9; dististyles evenly curving and tapering from a wide base to a narrow apex as seen from dorsal or ventral aspect, strongly curved ventrally from caudal aspect; parameres forming a long slender cone; aedeagus Y-shaped, the arms slightly modified apically.

Female genitalia: tergite 9 markedly longer than either tergite 7 or 8; sternite 8 slightly sinuous from lateral aspect, a deep V-shaped notch between subtriangular, apically rounded lobes.

Dimensions: wing length, ♂ 2.3–2.6 mm, ♀ 2.6 mm.

Distribution. New South Wales.

Etymology. The specific name is from the Latin adjective *sinuosus* (=sinuous), referring to details of tergite 9 in the male of this species.

Austrothaumalea spinosa n. sp.

Figs 67–71

Material examined. HOLOTYPE ♂: New South Wales, Pretty Point Creek, Mt Kosciusko, 13 Dec 1931, A.L. Tonnoir (ANIC). PARATYPES: New South Wales: 10 ♂, 2 ♀, same data as holotype (ANIC); 1 ♀, Brown Mountain, 25 Feb 1939, A.L. Tonnoir (ANIC); 1 ♂, 1 ♀, below Govetts Leap, Blue Mountains, 7 Dec 1956, D.K. McAlpine (AM); 6 ♂, Mt Kosciusko, 14 Feb 1934, 1 ♂, 1 ♀, same loc., 17 Feb 1938, A.L. Tonnoir (ANIC); 2 ♂, 2 ♀, Pretty Point Creek, 1615 m, Mt Kosciusko, 10 Dec 1931, c.u. (probably Tonnoir) (ANIC); 1 ♂, Sawpit Creek, Mt Kosciusko, 10 Nov 1960, E.F. Riek (ANIC). Tasmania: 1 ♂, Adventurers Bay, 30 Dec 1922, A. Tonnoir (ANIC); 2 ♂, 4 ♀, Burnie, 27 Oct 1922, 1 ♂, 1 ♀, same loc., 31 Jan 1923, 3 ♂, 1 ♀, same loc., 21 Oct 1933, A. Tonnoir (ANIC); 1 ♂, Fern Tree, 12 Nov 1922, A. Tonnoir (ANIC); 2 ♀, Weldboro Pass, 25 Oct 1933, A.L. Tonnoir (ANIC).

Description. Colouration: head dark brownish grey; thorax dark yellowish to medium brown; coxae, trochanters and femora yellowish brown, remaining leg segments medium brown to greyish black; wing and haltere yellowish to brownish grey; abdomen medium to dark greyish brown.

Wing: R_3 distinctly sinuous; $CuA + 1A$ slightly bent but with substantial appendix.

Male genitalia: tergite 9 with narrow median lobe flanked by one tooth on each side, these teeth elongate and pointed, and pointing towards each other below median lobe; basistyles reaching about level of lateral teeth of tergite 9; dististyles evenly curved and tapering from a moderately thick base into a narrow apical portion; parameres forming a single almost straight narrow stylet-shaped structure; aedeagus with narrow base and somewhat widened apical portion which is slightly notched posteromedially and covered with minute spines posterolaterally.

Female genitalia: tergite 9 longer than either tergite 7 or 8; sternite 8 with small subconical mediobasal protrusion, lobes evenly rounded, median notch generally U-shaped.

Dimensions: wing length, ♂ 2.4–3.0, ♀ 3.2–3.5 mm.

Distribution. New South Wales and Tasmania.

Etymology. The specific name is from the Latin adjective *spinus* (=thorny), referring to the spiny aedeagus of the male.

Austrothaumalea tasmanica n. sp.

Figs 72–76

Material examined. HOLOTYPE ♂: Tasmania, Hobart, 29 Oct 1933, A. Tonnoir (ANIC). PARATYPES: Tasmania: 2 ♂, 3 ♀, same data as holotype (ANIC); 2 ♂, Fern Tree, 10 Nov 1922, A. Tonnoir (ANIC); 1 ♂, Hobart, 3 Jan 1923, A.

Tonnoir (ANIC); 2 ♂, 1 ♀, Mount Wellington, 25–27 Nov 1922, A. Tonnoir (ANIC).

Description. Colouration: head dark brownish grey; thorax medium brown; coxae, trochanters and femora dull yellow, remaining leg segments yellowish to greyish brown; wing and haltere faint greyish brown; abdomen dark greyish brown.

Wing: R_3 sinuous; R_{4+5} with macrotrichia; CuA + 1A distinctly bent but without any sign of an appendix.

Male genitalia: tergite 9 posteriorly slightly convex, lateral corners distinctive but rounded, without teeth; basistyles not reaching posterior margin of tergite 9; dististyles with straight almost cylindrical basal half, strongly bent at about their middle, thence slightly

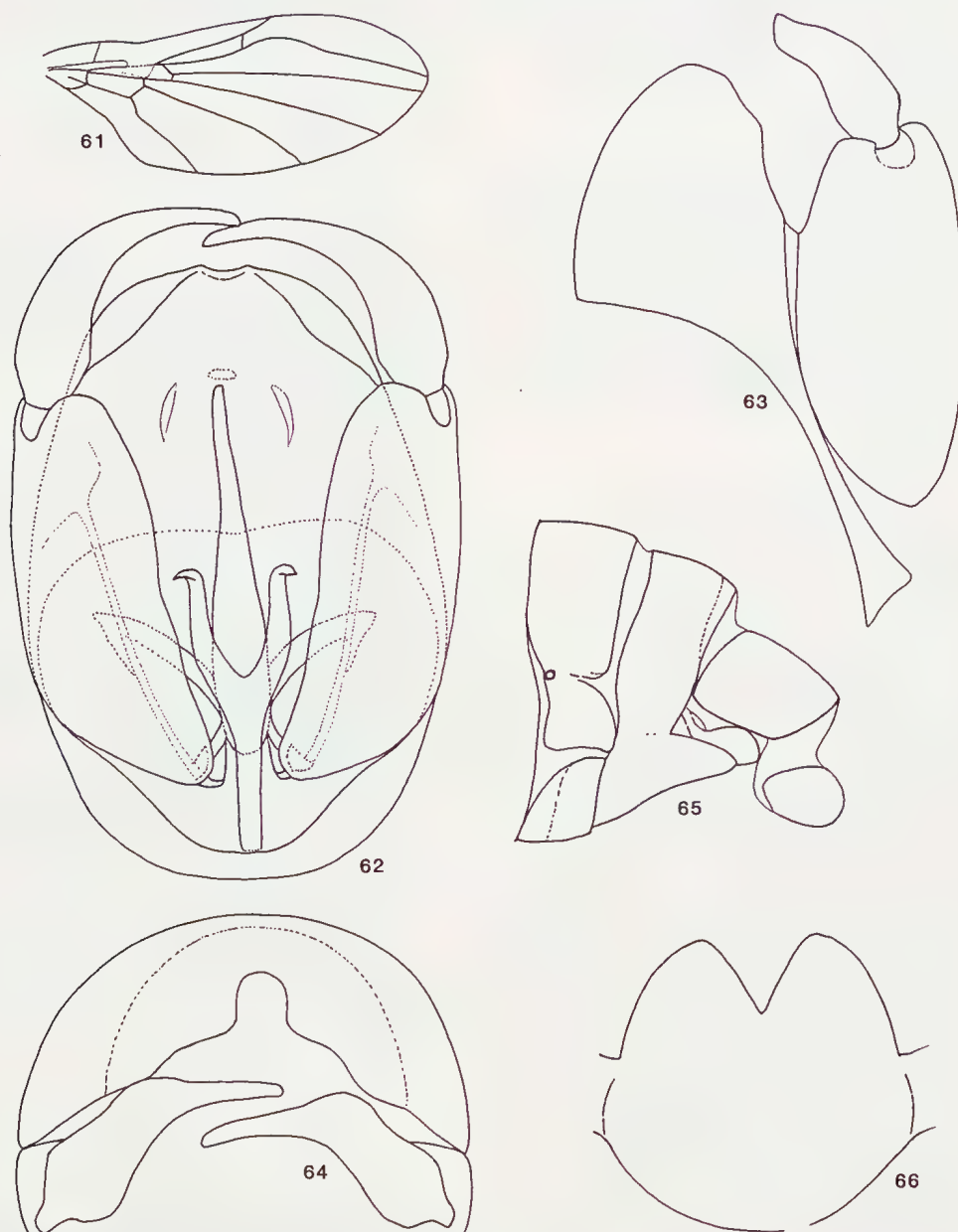
curved and tapering into a blunt hook; parameres forming an anchor-shaped structure with two peaks pointing anteroventrally; aedeagus Y-shaped with narrow base, arms evenly curved anteriorly.

Female genitalia: tergite 9 not longer than tergite 8; sternite 8 conspicuously bowed dorsally from lateral aspect, a wide V-shaped notch between subtriangular, apically rounded lobes which are much shorter than their basal width.

Dimensions: wing length, ♂ 2.7–3.0 mm, ♀ 3.0–3.7 mm.

Distribution. Tasmania.

Etymology. The specific name, meaning “from Tasmania”, is a latinized adjective, the species being known only from Tasmania.



Figs 61–66. *Austrothaumalea sinuosa* n. sp. 61–64, male: 61, wing; 62–64, genitalia: 62, ventral; 63, lateral; 64, caudal. 65, 66 female: 65, genitalia, lateral; 66, sternite 8.

Austrothaumalea tonnoiri n. sp.

Figs 77-81

Material examined. HOLOTYPE ♂: New South Wales, Belmore Falls, nr Robertson, 23 Jan 1963, D.H. Colless (ANIC). PARATYPES: New South Wales: 10 ♂, 1 ♀, same data as holotype (ANIC); 4 ♂, 1 ♀, Belmore Falls, nr Robertson, 2 Oct 1938, A.L. Tonnoir (ANIC); 5 ♂, 1 ♀, Fitzroy Falls, 22-27 Nov 1937, A.L. Tonnoir (ANIC); 1 ♀, Wentworth Falls, 18 Nov 1921, A. Tonnoir (ANIC).

Additional material. 2 ♀, New South Wales, Point Lookout, New England National Park, 12-22 Feb 1984, I.D. Naumann (ANIC).

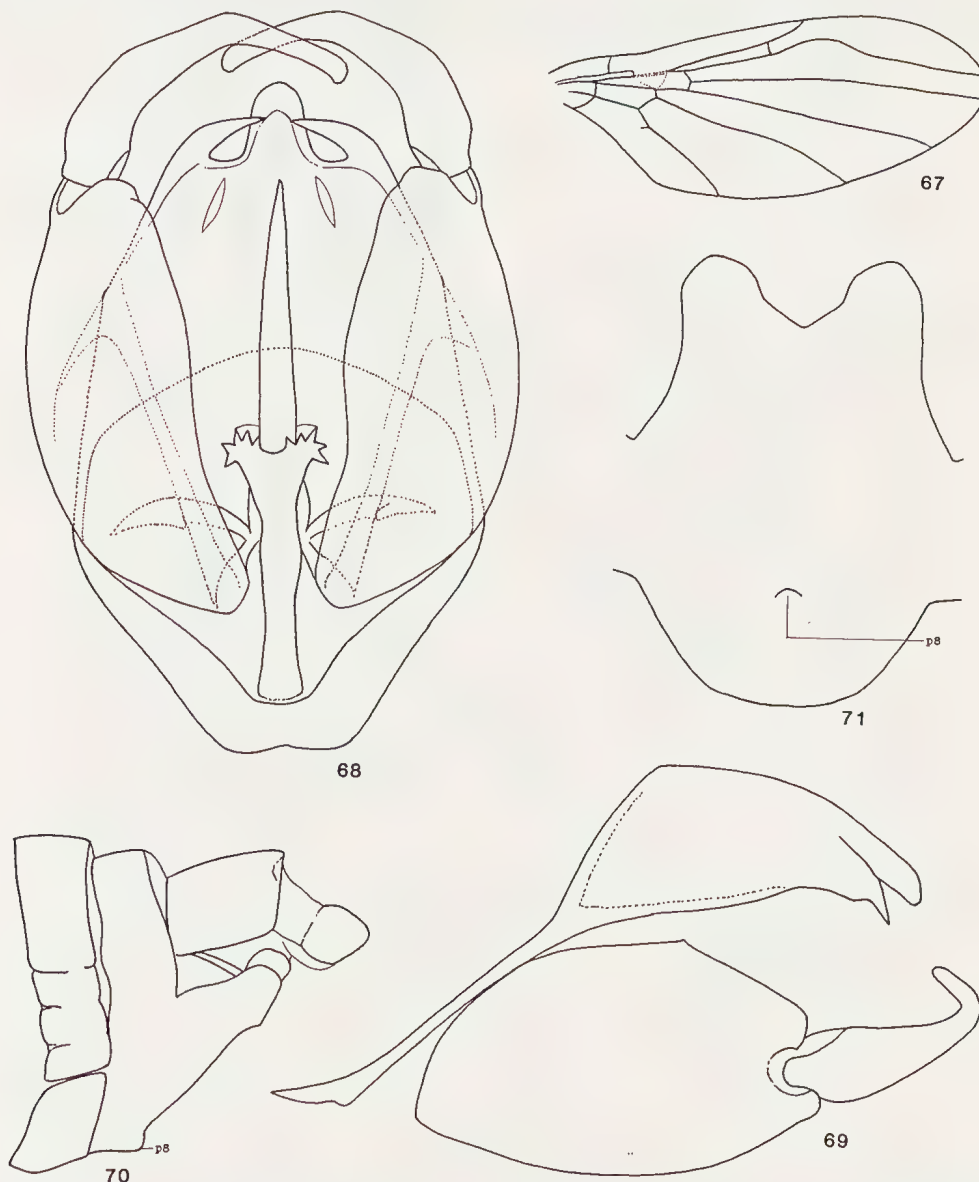
Description. Colouration: head greyish to brownish black; thorax dark yellowish to reddish, greyish or even blackish brown; coxae, trochanters and femora

yellowish to pale greyish brown, tibiae medium to blackish brown, remaining leg segments blackish brown; wing and haltere yellowish to pale greyish brown; abdomen medium to dark greyish brown.

Wing: R_3 very slightly sinuous; $CuA + 1A$ slightly bent and without any indication of an appendix.

Male genitalia: tergite 9 long, narrow, trapezoid, with posterior corners rounded, and no teeth or processes; basistyles reaching far short of posterior margin of tergite 9; dististyles long, curved, particularly at about midlength, very slightly tapered for basal $\frac{2}{3}$ of length, thence strongly tapered to form a narrow, weakly hooked tip; parameres forming a very long broad-based sigmoid cone with blunt tip; aedeagus short, appearing goblet-shaped from ventral aspect.

Female genitalia: tergite 9 markedly longer than



Figs 67-71. *Austrothaumalea spinosa* n. sp. 67-69, male: 67, wing; 68, 69, genitalia: 68, ventral; 69, lateral. 70, 71, female: 70, genitalia, lateral; 71, sternite 8. p8, protrusion of sternite 8.

tergite 8; sternite 8 widely and evenly curved dorsally from lateral aspect, a very shallow notch between very widely rounded, extremely short and wide lobes.

Dimensions: wing length, ♂ 2.2–2.8 mm, ♀ 2.8–3.1 mm.

Distribution. New South Wales.

Remarks. As males have not been collected together with the two females from north-eastern New South Wales, those specimens were not included in the type series.

Etymology. The species is dedicated to the late A.L. Tonnoir, in recognition of his invaluable collections of Australian Thaumaleidae.

Austrothaumalea uptoni n. sp.

Figs 82–85

Material examined. HOLOTYPE ♂: New South Wales, Clyde Mountain, 732 m, 17 Oct 1960, I.F.B. Common & M.S.

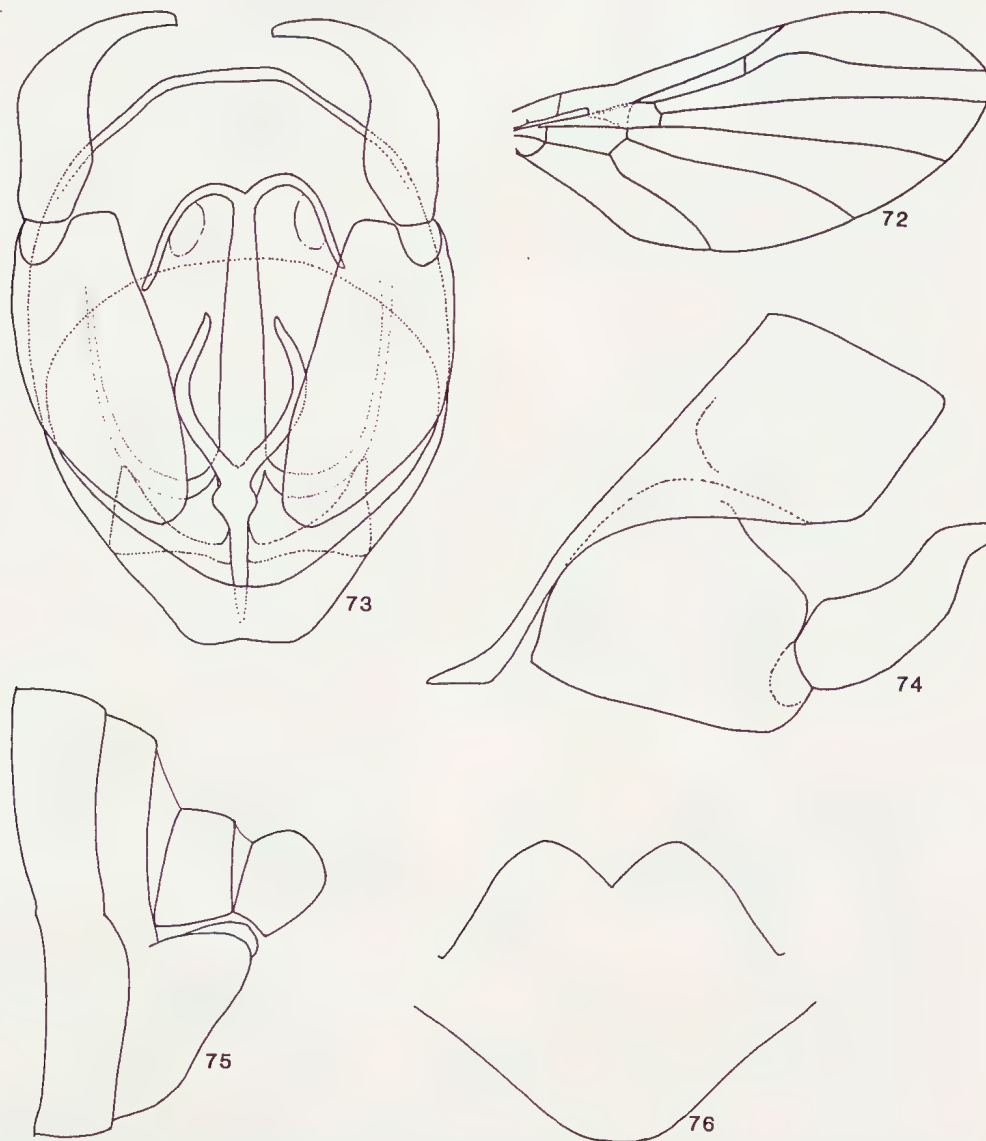
Upton (ANIC). PARATYPES: 1 specimen (abdomen missing), New South Wales, Clyde Mountain, 732 m, 21 Oct 1960, 1 ♂, same loc., 21 Mar 1961, I.F.B. Common & M.S. Upton (ANIC).

Description (male). Colouration: head blackish grey; thorax blackish brown; coxae, trochanters and femora medium brown, remaining leg segments greyish to blackish brown; wing and haltere pale greyish brown; abdomen dark greyish brown.

Wing: R_3 not sinuous; CuA + 1A distinctly bent and with substantial appendix.

Genitalia: tergite 9 wide, trapezoid with posterior corners slightly rounded; basistyles reaching far short of posterior margin of tergite 9; dististyles forked, with wide cylindrical base and short, narrow knob-like outer, and long tapering apically weakly hooked inner branch; parameres forming a short cone; aedeagus appearing broadly spoon-shaped from ventral aspect.

Dimensions: wing length 1.7–2.4 mm.



Figs 72–76. *Austrothaumalea tasmanica* n. sp. 72–74, male: 72, wing; 73, 74, genitalia: 73, ventral; 74, lateral. 75, 76, female: 75, genitalia, lateral; 76, sternite 8.

Distribution. New South Wales.

Etymology. The species is dedicated to Mr M.S. Upton, one of its collectors.

Austrothaumalea victoriae n. sp.

Figs 86-91

Material examined. HOLOTYPE ♂: Victoria, Sassafras, 19-20 Oct 1922, A. Tonnoir (ANIC). PARATYPES: 2 ♂, 3 ♀, same data as holotype (ANIC).

Additional material. Victoria: 1 ♀, Cumberland Creek, 24 Nov 1964, N. Dobrotworsky (ANIC); 1 ♀, Wilsons Promontory, Chinana Creek, 20 Nov 1964, N. Dobrotworsky (ANIC).

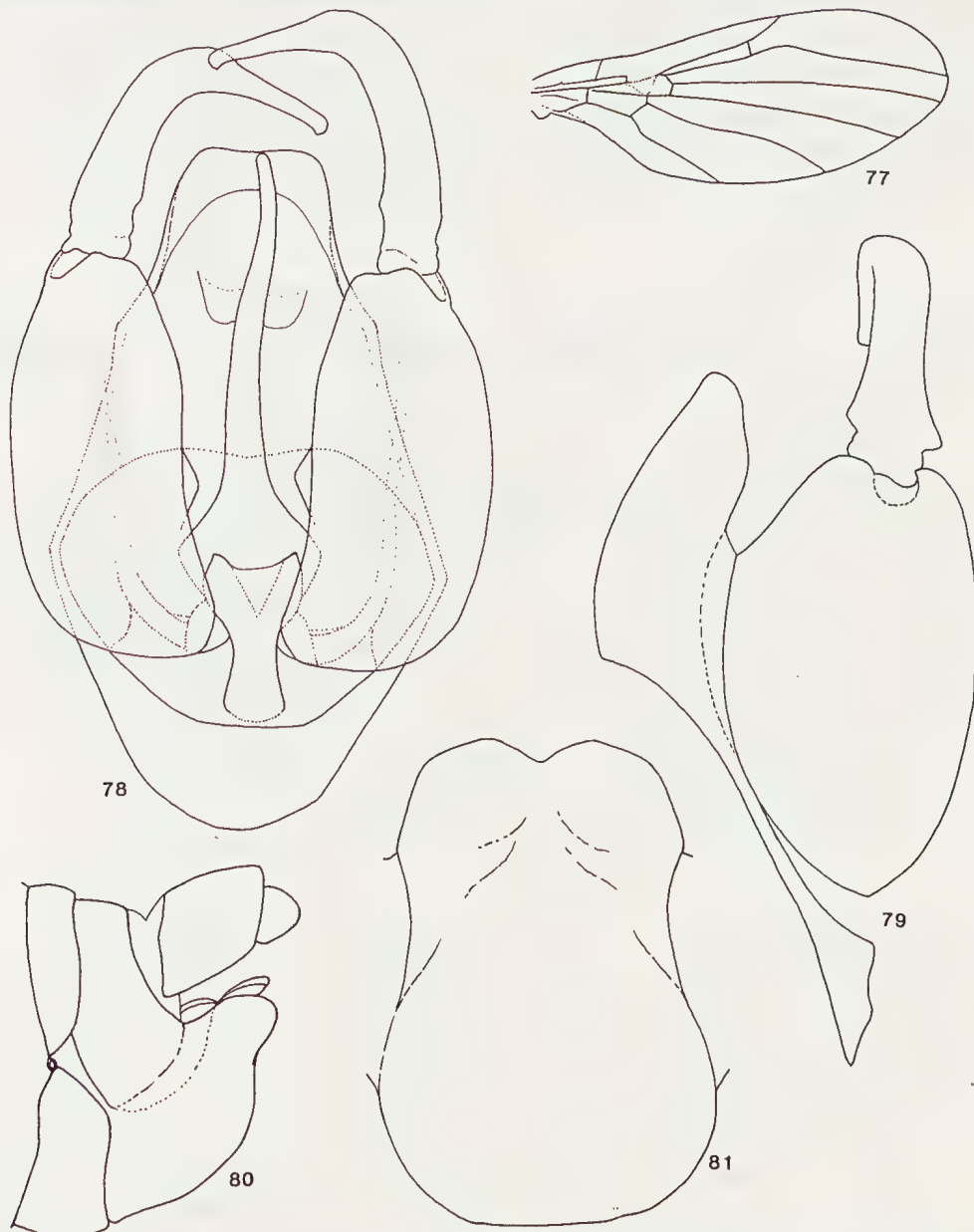
Description. Colouration: head dark greyish brown;

thorax brownish yellow; legs yellow to pale greyish brown; wing and haltere yellowish to greyish brown; abdomen pale to very dark greyish brown.

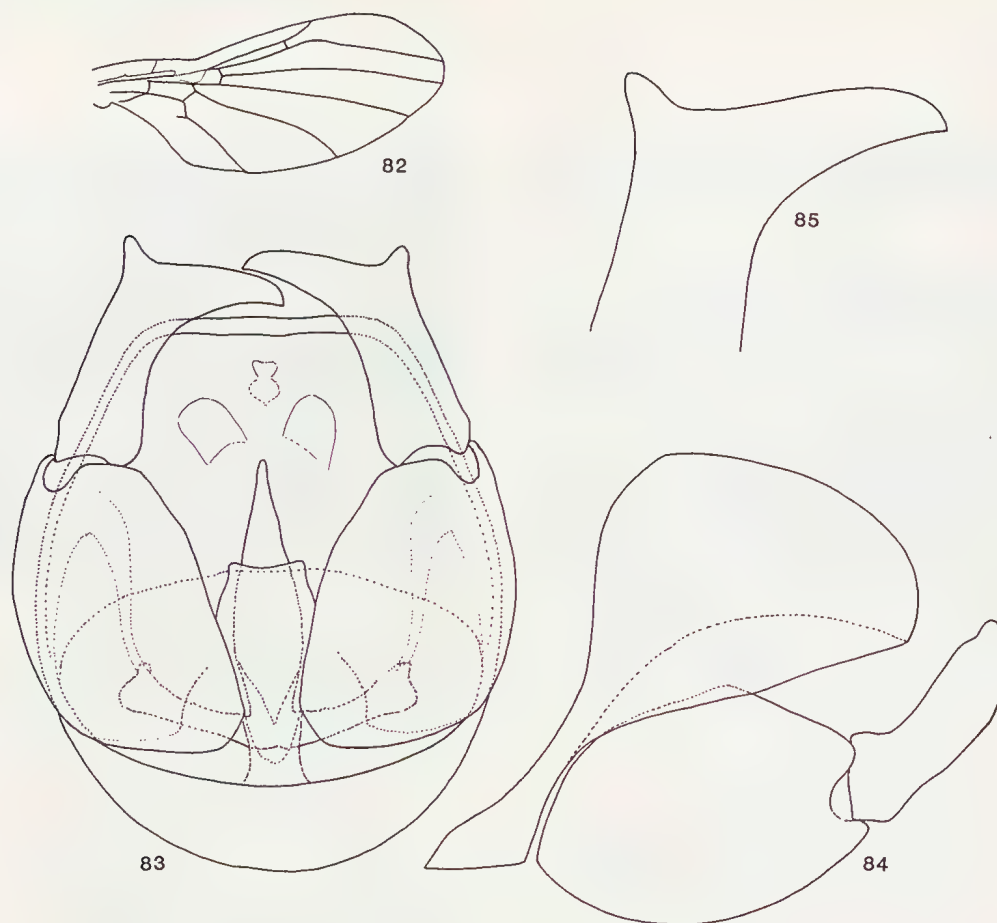
Wing: R_3 slightly sinuous; CuA + 1A distinctly bent and with small but distinct appendix.

Male genitalia: tergite 9 with almost straight posterior margin between the apical rounded corners, a small subapical tooth on each lateral margin; basistyles reaching about level of subapical lateral tooth of tergite 9; dististyles evenly curved, tapering into a moderately narrow apex; parameres forming a long narrow cone; aedeagus long and slender with slightly bifurcate apex.

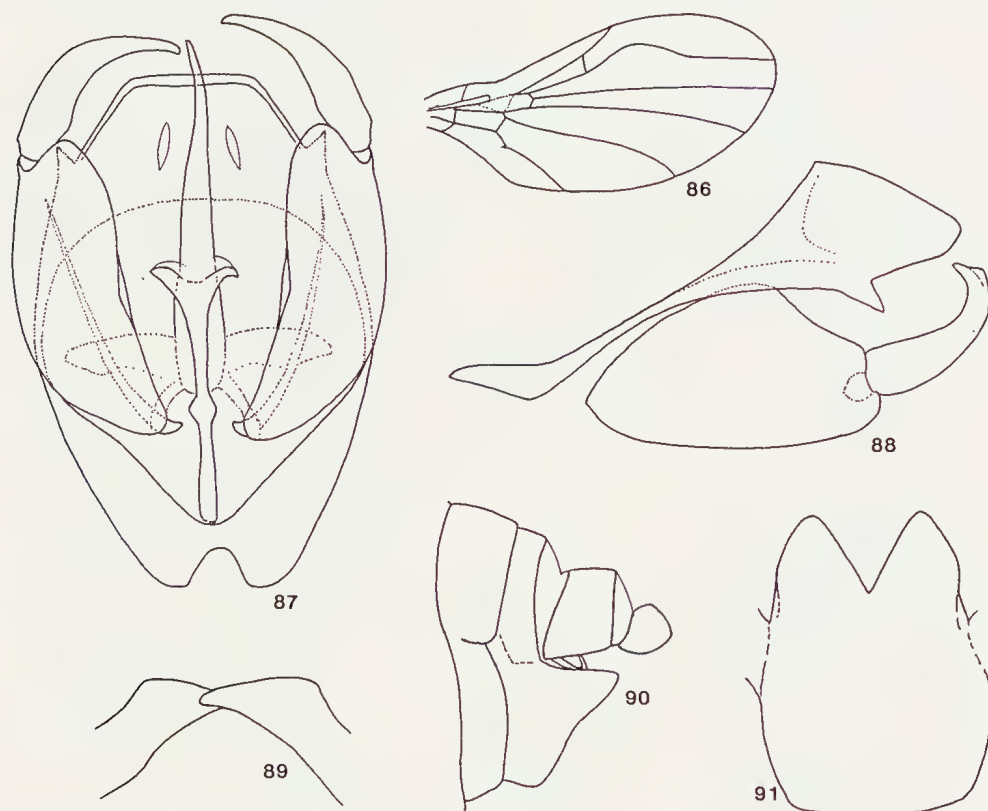
Female genitalia: tergite 9 longer than tergite 8; sternite 8 with moderately wide V-shaped notch between subtriangular, apically rounded lobes which are almost as long as their basal width.



Figs 77-81. *Austrothaumalea tonnoiri* n. sp. 77-79, male: 77, wing; 78, 79, genitalia: 78, ventral; 79, lateral. 80, 81, female: 80, genitalia, lateral; 81, sternite 8.



Figs 82-85. *Austrothaumalea uptoni* n. sp., male. 82, wing; 83,84, genitalia: 83, ventral; 84, lateral; 85, apical portion of dististyle.



Figs 86-91. *Austrothaumalea victoriae* n. sp. 86-89, male: 86, wing; 87,88, genitalia: 87, ventral; 88, lateral; 89, apical portion of dististyles, caudal. 90,91, female: 90, genitalia, lateral; 91, sternite 8.

Dimensions: wing length, ♂ 2.2–2.4 mm, ♀ 2.2–2.5 mm.

Distribution. Victoria.

Remarks. The identity of the two females which are not included in the type series is doubtful as males from the same localities are not available.

Etymology. The specific name refers to the state of Victoria where the material was collected.

Austrothaumalea zentae n. sp.

Figs 92–96

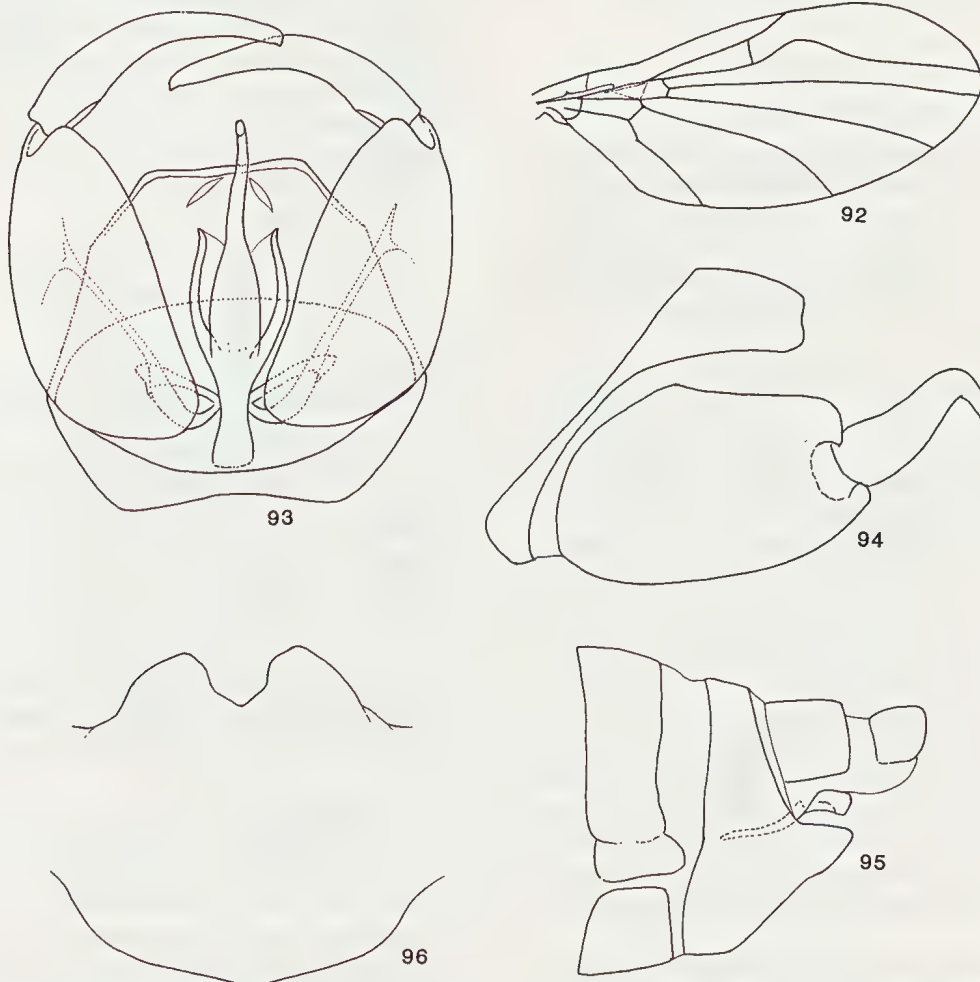
Material examined. HOLOTYPE ♂: New South Wales, Rutherford Creek, Brown Mountain, 17 July 1963, Z. Liepa (ANIC). PARATYPES: New South Wales: 2 ♂, 3 ♀, same locality and data as holotype, D.H. Colless (ANIC); 1 ♀, Brown Mountain, 25 Feb 1939, A.L. Tonnoir (ANIC); 4 ♀, Fitzroy Falls, 22–27 Nov 1937, 1 ♂, 1 ♀, same loc., 3 Oct 1938, A.L. Tonnoir (ANIC); 2 ♂, 1 ♀, Macquarie Pass, 2 Oct 1938, A.L. Tonnoir (ANIC); 1 ♂, McCarrs Creek, Kuring-gai Chase, 23 Sept 1962, D.H. Colless (ANIC); 1 ♂, Mt Kosciusko, 14 Feb 1934, A.L. Tonnoir (ANIC); 1 ♂, 2 ♀, Pacific Highway, 1.6 km south of Hawkesbury River, 29 Sept

1956, 1 ♂, same loc., 13 Oct 1956, D.K. McAlpine (AM); 4 ♂, 1 ♀, Rutherford Creek, Brown Mountain, 9 Aug 1962, 1 ♀, same loc., 15 Mar 1966, D.H. Colless (ANIC); 1 ♂, Sassafras Gully, Springwood, 23 Sept 1972, D.K. McAlpine (AM); 3 ♂, 5 ♀, Wentworth Falls, 18 Nov 1921, A. Tonnoir (ANIC); 2 ♂, same loc., 20 Nov 1959, D.K. McAlpine (AM); 2 ♂, Mount Wilson, 19 Nov 1933, A. Tonnoir (ANIC). Tasmania: 2 ♂, Adventurers Bay, 30 Dec 1922, A. Tonnoir (ANIC); 1 ♂, Burnie, 26 Nov 1922, A. Tonnoir (ANIC); 1 ♀, Cradle Valley, 10 Jan 1923, A. Tonnoir (ANIC); 1 ♀, Eaglehawk Neck, 22 Nov 1922, A.L. Tonnoir (ANIC); 3 ♂, Harz Mountains, 10 Dec 1922, A. Tonnoir (ANIC); 9 ♂, 9 ♀, Maria Island, 6 Nov 1933, A. Tonnoir (ANIC); 3 ♂, 1 ♀, St Patrick, 31 Oct & 1 Nov 1922, A. Tonnoir (ANIC); 1 ♂, Weldboro Pass, 25 Oct 1933, A.L. Tonnoir (ANIC).

Additional material. 2 ♀, New South Wales, Tubrabucca Falls, 16 Nov 1953, A. Neboiss (MV).

Description. Colouration: head greyish brown; thorax brownish yellow to dark ochreous; coxae, trochanters and femora pale brownish yellow, tibiae yellowish brown to greyish brown, remaining leg segments brownish grey; wing and haltere yellowish to brownish grey; abdomen dull yellowish brown to greyish black.

Wing: R_3 strongly sinuous; $CuA + 1A$ distinctly



Figs 92–96. *Austrothaumalea zentae* n. sp. 92–94, male: 92, wing; 93, 94, genitalia: 93, ventral; 94, lateral. 95, 96, female: 95, genitalia, lateral; 96, sternite 8.

angulated, with or without slight indication of an appendix.

Male genitalia: tergite 9 widely trapezoid with lateral corners rounded from dorsal and lateral aspect, no teeth or processes; basistyles reaching beyond posterior margin of tergite 9; dististyles slightly arched and gradually tapering from a moderately wide base into a narrow, slightly hooked tip; parameres forming a basally swollen, otherwise narrow and slightly sigmoid structure with blunt tip; aedeagus Y-shaped, with base short and branches curved.

Female genitalia: tergite 9 markedly longer than tergite 8; sternite 8 conspicuously bowed dorsally from lateral aspect, a wide almost U-shaped notch between widely rounded, somewhat medially directed lobes.

Dimensions: wing length, ♂ 1.9–2.6 mm, ♀ 2.4–3.2 mm.

Distribution. New South Wales and Tasmania.

Remarks. As males from Tubrabucca Falls are not available, the females from this locality were not included in the type series.

Etymology. This species is named after Ms Zenta Liepa in recognition of the help that she has given me.

Niphta n. gen.

Type species. *Niphta bickeli* n. sp.

Description. Mesothorax with strongly developed, short antealar ridge on each side. Abdomen of male with tergites 1–9 and sternites 1–8 developed; tergite 9 without ventral bridge (i.e. sternite 9). Tergites and sternites 1–9 developed in the female. Pubescence much as in *Austrothaumalea*, in addition large bristles on antealar ridge.

Wings: much as in *Austrothaumalea*, with the following differences: tip narrowly rounded; macrotrichia present but sparse on C, very sparse on remaining wing margin and on R_{1+2} (very few only), immediately beyond level of humeral crossvein; humeral crossvein at the level of proximal side of basal cells; R_3 widely and evenly arched posteriorly; free transverse section of R_2 markedly closer to the origin of R_{2+3} than to the end of R_{1+2} ; R_{4+5} very slightly arched anteriorly; M_{1+2} almost straight; $CuA + 1A$ angulated and bent anteriorly at about the level of crossvein $m-cu$; no appendix at this bend.

Male genitalia: tergite 9 very wide and short, without ventral bridge; basistyles reaching beyond posterior margin of tergite 9, attached by membrane to sternite 8; parameres fused medially to form a symmetrical structure consisting at least of a median part which is bent ventrally; two sclerotized rods running towards posterior margin of tergite 9; aedeagus apparently not developed.

Female genitalia: sternite 7 not significantly modified; sternite 8 strongly modified, bilobed, markedly wider than long; sternite 9 highly modified, strongly sclerotized and generally largely covered by lobes of

sternite 8; tergite 9 much longer than tergite 8, with posterolateral corners produced but evenly rounded.

Etymology. The generic name is an arbitrary combination of letters. Its gender is feminine.

Niphta bickeli n. sp.

Figs 97–102

Material examined. HOLOTYPE ♂: New South Wales, Dorrigo, Newell Falls, 12 Oct 1962, D.H. Colless (ANIC). PARATYPES: New South Wales: 1 ♀, same data as holotype (ANIC); 1 ♀, Dorrigo National Park, 22–23 Oct 1980, D.J. Bickel (ANIC).

Description. Colouration: head, thorax and abdomen greyish to blackish brown; legs yellowish to dark greyish brown; wing and haltere dark yellowish to brownish grey.

Male genitalia: tergite 9 with posterior margin straight laterally, and with a posteriorly wide, anteriorly narrow, roughly V-shaped cleft medially; basistyles wide and short; dististyles hook-like with very small inner subapical tooth and large apical spur; parameres forming only a median tap-like structure.

Female genitalia: sternite 8 with triangular lobes wide and almost as long as sternite along midline.

Dimensions: wing length, ♂ 2.8 mm, ♀ 2.9–3.5 mm.

Distribution. New South Wales.

Etymology. The species is dedicated to Dr D.J. Bickel, one of its collectors.

Niphta collessi n. sp.

Figs 103–106

Material examined. HOLOTYPE ♂: Australian Capital Territory, Mount Gingera, 20 Nov 1960, D.H. Colless (ANIC).

Description (male). Colouration: head, greyish black; thorax greyish to blackish brown; legs brownish yellow to greyish brown; wing and haltere dark yellowish to brownish grey; abdomen medium to blackish brown.

Genitalia: tergite 9 from dorsal aspect almost semicircular with posterior margin very slightly undulate and very weakly sclerotized posteromedially; basistyles short and very wide; dististyles long, wide at base, tapering to a thin spine which is slightly bent at about half length; parameres forming a tap-like median structure flanked by a horn-shaped structure on each side.

Dimensions: wing length uncertain (wings partly destroyed), however, the species is rather large; remaining wing parts suggest a length of about 3.2 mm.

Distribution. New South Wales.

Etymology. The species is dedicated gratefully to Dr D.H. Colless, in recognition of the invaluable contribution made by his extensive collecting of Australian Thaumaleidae and the help and encouragement he has given me.

Niphta farecta n. sp.

Figs 107–112

Material examined. HOLOTYPE ♂: New South Wales, Fitzroy Falls, 22–27 Nov 1937, A.L. Tonnoir (ANIC). PARATYPES: New South Wales: 1 ♂, Belmore Falls, 2 Oct 1938, A.L. Tonnoir (ANIC); 2 ♀, Macquarie Pass, 2 Oct 1938, A.L. Tonnoir (ANIC); 1 ♀, Sydney, Terrey Hills, 14 Sept 1963, D.H. Colless (ANIC).

Description. Colouration: head and thorax greyish to blackish brown; legs yellowish to greyish brown; wing and haltere dark yellowish to brownish grey; abdomen medium to greyish brown.

Male genitalia: tergite 9 very wide with median third produced posteriorly, strongly sclerotized except for a

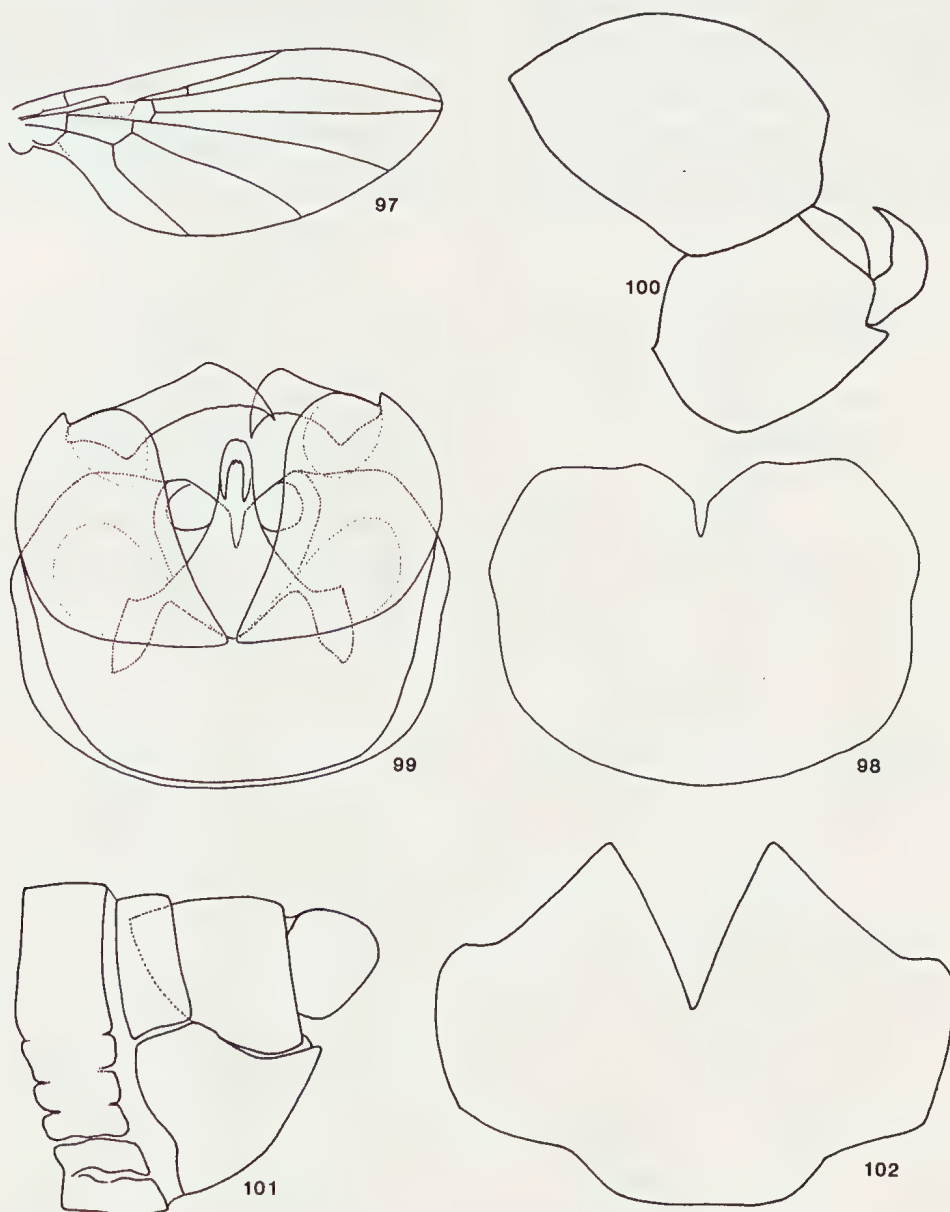
narrow median wedge; basistyles wide and short, with short rounded inner appendix and stylet-shaped outer process; dististyles with widely rounded and rather flat membranous portion and, along its margins, with highly arched lanceolate sclerotized portion; parameres forming a bird-head-like median structure, with a long straight spine on each side at its base.

Female genitalia: sternite 8 with triangular lobes narrow and markedly shorter than sternite along midline.

Dimensions: wing length, ♂ 2.0–2.1 mm, ♀ 2.4–2.5 mm.

Distribution. New South Wales.

Etymology. The specific name is an arbitrary combination of letters and is indeclinable.



Figs 97–102. *Niphta bickeli* n. sp. 97–100, male: 97, wing; 98, tergite 9; 99, 100, genitalia: 99, ventral; 100, lateral. 101, 102, female: 101, genitalia, lateral; 102, sternite 8.

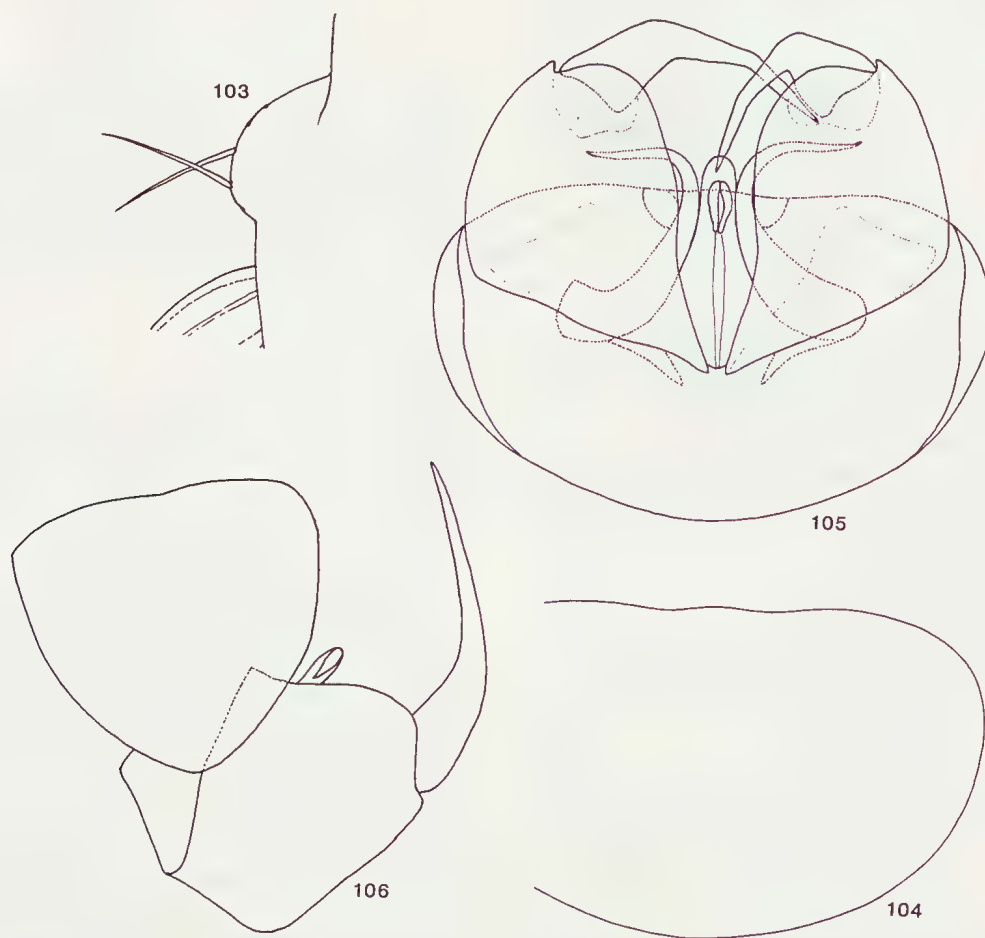
Affinities of the Australian Thaumaleidae

The known Australian Thaumaleidae (genera *Austrothaumalea* and *Niphta*) show close affinities to other southern hemisphere Thaumaleidae only. All Australian species of *Austrothaumalea* seem closely related to *A. neozealandica* Tonnoir, the type species of the genus, to *A. appendiculata* Tonnoir, to several other species from New Zealand (being described by McLellan) and to some of the species described under *Austrothaumalea* from South America (*A. chilensis* Edwards, *A. apicalis* Edwards, *A. spatulata*, described by Schmid, 1970). Only one Australian species of *Austrothaumalea*, *A. tasmanica* n. sp., deviates from typical *Austrothaumalea* in the wing setation (macrotrichia additionally on R_{4+5}) and, in this respect, corresponds with a new genus from New Zealand (McLellan, personal communication) and with *A. setipennis* Edwards from South America. However, whereas McLellan's new genus and *A. setipennis* also differ significantly from *Austrothaumalea* in male genitalia, *A. tasmanica* has male genitalia typical for *Austrothaumalea*. How close *Niphta* is to *Afrothaumalea* Stuckenberg is hard to tell because of

insufficient material of *Afrothaumalea*. However, the species of *Niphta* appear very similar to *Austrothaumalea halteris* Edwards and *A. nudipennis* Edwards from South America, both of which are considered here to be extra-limital members of *Niphta* [*Niphta halteris* (Edwards) n. comb., *Niphta nudipennis* (Edwards) n. comb.]. In fact, the Australian *Niphta farecta* n. sp. appears closer to *N. nudipennis* than to any Australian species.

All those affinities, together with the predominantly southern distribution of Thaumaleidae in Australia, suggest a southern origin (Gondwana) of all Australian forms and indicate a remarkable age even for units of low taxonomic rank.

ACKNOWLEDGEMENTS. I wish to thank all persons who supported this study by providing information and suggestions or by the loan of material in their care. They are Dr D.J. Bickel and Dr D.K. McAlpine (Sydney); Dr D.H. Colless, Miss Z. Liepa and Dr I.D. Naumann (Canberra); Mr I.D. McLellan (Westport, New Zealand), Dr A. Neboiss (Melbourne), Dr B.V. Peterson (Washington D.C., USA) and Dr B.R. Stuckenberg (Pietermaritzburg, South Africa).

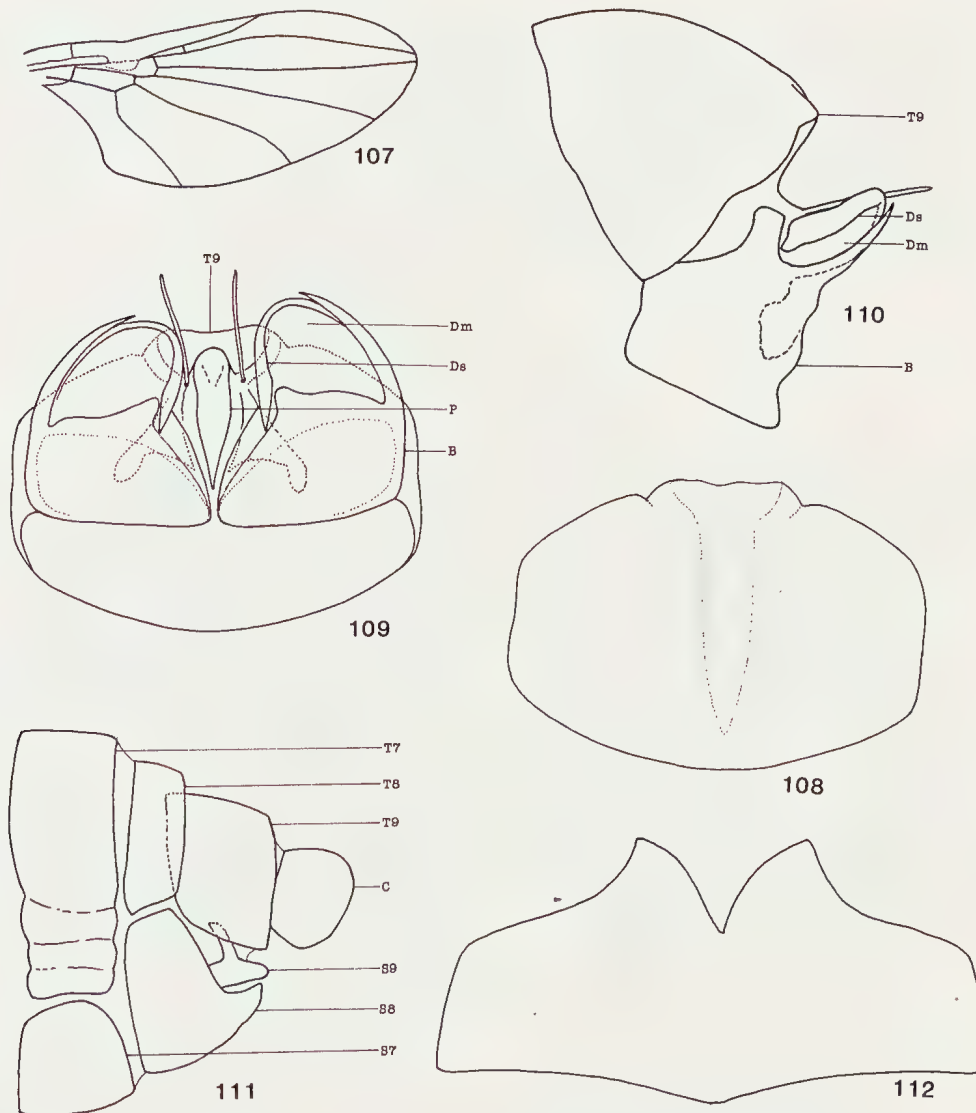


Figs 103–106. *Niphta collessi* n. sp., male. 103, left side of thorax and wing base, dorsal; 104, tergite 9 (in part); 105, 106, genitalia: 105, ventral; 106, lateral.

References

- Arnaud, P.H., 1977. Thaumaleidae. Pp. 283-285, in "Biota Acuatica de Sudamerica Austral" (S.H. Hurlbert, ed.), xiv + 342 pp. San Diego State University, San Diego.
- Colless, D.H. & D.K. McAlpine, 1970. Diptera (Flies). Pp. 656-740, in "The Insects of Australia", xiii-1029 pp. Melbourne University Press, Melbourne.
- Edwards, F.W., 1929. A revision of the Thaumaleidae (Dipt.). Zoologischer Anzeiger (Wasmann-Festband) 82: 12-142.
- 1930. Bibionidae, Scatopsidae, Cecidomyiidae, Culicidae, Thaumaleidae (Orphnephilidae), Anisopodidae (Rhyphidae). Diptera of Patagonia and South Chile 2 (3): 77-119, pls 9-11. British Museum (Natural History), London.
- McLellan, I.D., 1983. New diagnosis for genus *Austrothaumalea*, and redescription of *A. neozealandica* (Diptera: Thaumaleidae). New Zealand Journal of Zoology 10: 267-270.
- Schmid, F., 1970. Quelques Thaumaleides nouvelles ou peu connues (Diptera: Thaumaleidae). Naturaliste Canadian 97 (5): 499-510.
- Stone, A., 1966. Family Thaumaleidae (Orphnephilidae), fasc. 13: 1-2, in "A catalogue of the Diptera of the Americas south of the United States". Departamento de Zoologia, Secretaria da Agricultura, Sao Paulo.
- Stuckenberg, B.R., 1960. A new genus and species of Thaumaleidae from South Africa (Diptera). Proceedings of the Royal Entomological Society, London (B) 29, pls 7 and 8: 107-109.
- 1961. Chapter vi. Diptera (Nematocera): Thaumaleidae. Pp. 409-412, in "South African Animal Life. Results of the Lund University Expedition in 1950-1951" (B. Hanström, P. Brinck & G. Rudbeck, eds). Volume 8: 557 pp. Almqvist & Wiksell, Goteborg, Stockholm, Uppsala.
- Tonnoir, A.L., 1927. Descriptions of new and remarkable New Zealand Diptera. Records of the Canterbury Museum 3: 101-112.

Accepted 13th May 1986



Figs 107-112. *Niphta farecta* n. sp. 107-110, male: 107, wing; 108, tergite 9; 109, 110, genitalia: 109, ventral; 110, lateral. 111, 112, female: 111, genitalia, lateral; 112, sternite 8. B, basistyle; C, cercus; D, dististyle; S, sternite; T, tergite.

The Polycirrinae (Polychaeta: Terebellidae) from Australia

PAT HUTCHINGS AND CHRIS GLASBY

Australian Museum,
P.O. Box A285, Sydney South, NSW 2000, Australia

ABSTRACT. The polycirrine fauna of Australia comprises four genera and 22 species. These are described, and a key to the genera and Australian species are provided. Eleven new species are described: *Hauchiella renilla* n. sp., *Lysilla laciniata* n. sp., *L. bilobata* n. sp., *L. jennacubinae* n. sp., *Polycirrus bicrinalis* n. sp., *P. disjunctus* n. sp., *P. nephrosus* n. sp., *P. parvus* n. sp., *P. paucidens* n. sp., *P. tessellatus* n. sp. and *P. variabilis* n. sp., and the following new combinations, *Amaeana apheles* (Hutchings) and *Polycirrus octosea* (Hutchings). A full description of all Australian species of this subfamily is given except when a recent full description is available. Comments are made on the variety of characters which have been used to describe species of *Polycirrus* and the value of these characters.

HUTCHINGS, P.A. & C.J. GLASBY, 1986. The Polycirrinae (Polychaeta: Terebellidae) from Australia. Records of the Australian Museum 38(6): 319–350.

The Polycirrinae recorded from Australia prior to 1979 are listed by Day & Hutchings (1979) and include six species belonging to four genera. In 1984 we began a revision of the family Terebellidae (Hutchings & Glasby, 1986, in press), and by examining all the collections of terebellids housed in Australian Museums we have considerably expanded the polycirrine fauna of Australia. In this paper we describe 11 new species and synonymise the genus *Litancyra* Hutchings with the genus *Polycirrus* Grube.

The sizes of animals examined were measured as total body length excluding tentacles, maximum body width excluding notopodia, and the number of body segments. The Australian distribution of each species is indicated at the end of each species account, and exact localities are shown in Fig. 12. In cases where species are recorded from outside Australia, all existing records are indicated.

The following abbreviations have been used.

AHF Allan Hancock Foundation, Los Angeles
AM Australian Museum, Sydney
BMNH British Museum Natural History, London
CSIRO Commonwealth Scientific and Industrial Research Organisation, North Beach, Perth

HZM Zoologisches Institut und Zoologisches Museum der Universität, Hamburg
NMV National Museum of Victoria, now Museum of Victoria
NMW Naturhistorisches Museum, Wien
NSWSF New South Wales, Department of Agriculture, Fisheries Division
QM Queensland Museum, Brisbane
USNM National Museum of Natural History, Smithsonian Institution, Washington
UZM Universitets Zoologiska Museum, Uppsala
WAM West Australian Museum, Perth
ZMA Zoologisch Museum, Amsterdam
ZMB Zoologisches Museum, Museum für Naturkunde der Humboldt — Universität, Berlin
ZMO Zoologisk Museum, Oslo

Polycirrinae (Malmgren)

Polycirridae Malmgren, 1865: 390.—Caullery, 1944: 189–191.
Polycirrinae Hesse, 1917: 219.

Description. Expanded tentacular membrane. Branchiae absent. Notopodia if present with capillary

setae often ornamented. Neuropodia if present with either elongated avicular uncini or short acicular spines. Neurosetae always arranged in single rows and neuropodial tori poorly developed. All types of setae may be completely absent.

Comments. We have followed the definition of Polycirrinae given by Hessle (1917) and subsequently

used by Fauchald (1977): all members of this subfamily lack branchiae and thoracic uncini (if present) occur in single rows. We have rejected Day's (1967) revised definition of Polycirrinae, which included all abbranchiate genera regardless of the arrangement of the uncini, since we consider the arrangement of the uncini to be a far more important character than the presence or absence of branchiae.

Key to the genera of Polycirrinae (after Fauchald, 1977)

1. Setae lacking on all segments. *Hauchiella*
— Setae present on some segments. 2
2. Neurosetae lacking on all setigers. 3
— Neurosetae present on some setigers. 4
3. Thoracic notopodia vascularised and in part furcate or branched. *Enoplobranchus**
— Thoracic notopodia sometimes vascularised but never branched or furcate. *Lysilla*
4. Neurosetae short handled uncini, present on thorax and or abdomen. *Polycirrus*
— Neurosetae long handled spines, present only on abdomen. *Amaeana*

*Genus not recorded from Australia.

Amaeana Hartman

Amaea Malmgren, 1866: 392.

Amaeana Hartman, 1959: 495.

Type species. *Polycirrus trilobata* Sars, 1863, designated by Malmgren 1866.

Description. Tentacular membrane trilobed. Nine to 13 thoracic segments; notopodia from segment 3, with smooth or barbed notosetae. Thoracic neurosetal uncini absent; abdominal neurosetae long shafted spines.

Comments. The genus *Amaeana* in Australia is

represented by two estuarine species, *A. apheles* (Hutchings) new combination and *A. trilobata* (Sars), and one marine species *A. antipoda* (Augener). All species occur widely although discontinuously, and *A. apheles* and *A. trilobata* occur in the same habitat. The discontinuous distributions of all three species, especially marked for *A. antipoda*, reflects the sparse offshore collecting so far carried out in Australia.

To date, three of the six known species of *Amaeana* have been recorded from Australian waters: *A. apheles* is restricted to Australia, *A. antipoda* to Australasia and *A. trilobata* has apparently a cosmopolitan distribution.

Key to Australian species of *Amaeana*

1. 11 pairs of notopodia; notosetae smooth, wingless capillaries. *A. antipoda*
— 9–10 pairs of notopodia; notosetae smooth, wingless capillaries. 2
2. Achaetous region of 3–8 segments between thorax and abdomen; 9–10 pairs of notopodia. *A. apheles*
— Achaetous region of about 12 segments between thorax and abdomen; 10 pairs of notopodia. *A. trilobata*

Amaeana antipoda

Figs 1a,b; 12A

Amaea antipoda Augener, 1926: 241, fig. 17.

Material examined. Western Australia: Dampier

Archipelago, Mermaid Sound 2(WAM 17-84). Queensland: Great Barrier Reef, Stn D25 (16°40.7'S 146°1.0'E), 1(BMNH ZB 1985.220); Stn D26 (16°41.1'S 146°0.8'E) 2(BMNH ZB 1985.222). One complete specimen (BMNH ZB 1985.220), about 56 segments, 21 mm long, 1.1 mm maximum width.

Description. Body with swollen, papillate thorax; long, tapering abdomen. Irregular patches of brown pigment scattered over body. Midventral groove deep on thorax, more shallow on abdomen, containing a series of narrow, glandular ventral pads. Thoracic notopodia slender, cylindrical, decreasing in length slightly after first few, total of 11 pairs. Notoetae fine, smooth capillaries, without wings (Fig. 1a), arranged in a single tier, increasing in length distally. Nephridial papillae small, present at base of each notopodium. Gonopores present on setigers 4–8 in mature specimens. Achaetous region extending posteriorly from thorax for 6–8 segments, approximately equal in length to thoracic region. Abdominal neuropodia papilliform, approximately 36 pairs; neurosetae slightly tapered, slender, acicular spines with blunt tips (Fig. 1b), 2–3 per fascicle.

Remarks. The present material agrees well with Augener's description. This is the first record of this species from Australia, which was previously known only from Lyttelton, New Zealand.

Habitat. Queensland material found in 22 and 27 m in calcareous mud with many bivalves (D25), and muddy sand with many foraminiferans (D26).

Distribution. Western Australia and Queensland (Fig. 12A). Lyttelton, New Zealand.

Amaeana apheles new combination

Figs 1c–e; 12A

Lysilla apheles Hutchings, 1974: 190–191, fig. 5A; 1977: 10–11.—Hutchings & Murray, 1984: 90.

Amaeana trilobata.—Hutchings, 1977: 9 (in part). Not Sars.

Material examined. HOLOTYPE (AM W5239), PARATYPES (AM W5237, W5238) from Wallis Lake, New South Wales. Western Australia: North West Shelf, off Port Hedland, many (AM W199562), many (AM W199580). New South Wales: Hawkesbury River 1(AM W195861), 1(AM W195875), 4(AM W195878). Queensland: Moreton Bay, Stn 46, 1(AM W7086), Stn 47, 1(AM W7095), Stn 54, 1(AM W7093); Nerang River 1(AM W10864); Calliope River 2(AM W8519), 3(AM W10338), 3(AM W13480), 1(AM W13482); Auckland River 1(AM W13187); Gladstone, 59(AM W199448); Mary River, Kangaroo Island 3(AM W5384); Townsville, Halifax Bay 3(AM W199446), 4(AM W199444), 1(AM W199440), 12(AM W199447), 2(AM W199445), 2(AM W199441), 1(AM W199439). Specimens mostly incomplete, range in width from 0.9–2.1 mm. Material examined from North West Shelf represents a selection of that available.

Description. Thorax with 9–10 pairs of notopodia from segment 3; last 1–2 pairs reduced in size; notosetae smooth capillaries, appearing very narrowly winged under 100x (Fig. 1c,d). Thorax without neuropodia. Achaetous region with about 12 segments, 1–2 times length of thorax. Abdomen with papilliform neuropodia, up to 70–80 pairs; neurosetae robust, highly tapered acicular spines, 1–2 spines per fascicle (Fig. 1e).

Remarks. Type material of *Lysilla apheles* Hutchings, 1974, from Wallis Lake and other material from

Moreton Bay (Hutchings, 1977) was re-examined. All specimens lacked the posterior part of the abdomen and therefore the abdominal neurosetae. Hutchings (1977) referred the specimens to the genus *Lysilla*, since they lacked branchiae, thoracic neurosetae and apparently also lacked abdominal neurosetae. Examination of whole specimens from similar environments on the east coast of Australia showed that the species does have abdominal neurosetae, which are absent from an initial achaetous abdominal region of up to twice the length of the thorax. *Lysilla apheles* is therefore transferred to the genus *Amaeana*.

The abdominal neurosetal spines of *A. apheles* are relatively thick at the base and highly tapered, and there are usually only 1–2 per neuropodial fascicle. *Amaeana trilobata* (Sars), a widespread Australian species, has 3–15 spines per neuropodial fascicle, and the spines are more slender than those found in *A. apheles* and a shorter achaetous region. Where the two species co-occur, such as in the Hawkesbury and Calliope Rivers and on the North West Shelf, they may also be distinguished by size and colouration. Preserved specimens of *A. apheles* are often smaller and more highly pigmented (brown-purple) than *A. trilobata*. The variation in the number of pairs of notopodia does not appear to be related to the size of the animal.

Amaeana apheles differs from other species in the genus in the number of pairs of notopodia and type of thoracic notosetae. *Amaeana accraënsis* (Augener, 1918) has 11–13 pairs of notopodia with smooth and barbed notosetae; *A. antipoda* (Augener, 1926) has 11 pairs of notopodia with smooth notosetae; and *A. occidentalis* (Hartman, 1944) has 12 pairs of notopodia with smooth notosetae (see key in Hartman, 1944). *Amaeana coleii* (McIntosh, 1926) is known only from an anterior fragment of 5–6 segments. Its generic status is questionable as the type description equally well fits the genus *Lysilla*.

Habitat. Estuarine and protected marine embayments; often amongst seagrass beds; in 40–80 m on North West Shelf in sandy and gravelly sand sediments.

Distribution. Western Australia, New South Wales and Queensland (Fig. 12A).

Amaeana trilobata

Figs 1f–i; 12A

Polycirrus trilobatus Sars, 1863: 305.

Amaeana trilobata.—Malmgren, 1866: 392, pl. XXV fig. 70; Fauvel, 1927: 285–286, fig. 99a–c.

Amaeana trilobata.—Day, 1961: 533–534; 1967: 718–719, fig. 36.3e–h; 1973: 122, fig. 16d–f; Hutchings, 1977: 9 (in part); Hutchings & Murray, 1984: 90.

Material examined. TYPES (ZMO C3207a,b C3208) Christiansund (Største eks); Slaatholmen i Lofoten (de 2 minster) and Drøbak, Norway. Western Australia: North West Shelf, off Port Hedland 1(AM W199557). South Australia: Streaky Bay, Little Beach 1(AM W199014); Robe, Karatta

Beach 1(AM W199018). Victoria: Port Phillip Bay 1(AM W16115), 1(AM W16116); Western Port Bay 8(NMV F50357), 6(NMV F50356); Bass Strait 1(NMV F50355), 1(NMV F50354). Tasmania: Maria Island 1(AM W199019). New South Wales: Port Hacking 1(AM W195239); Botany Bay 1(AM W195744); Hawkesbury River 1(AM W195869), 2(AM W195860); South West Solitary Island 1(AM W199030); Lennox Head 1(AM W199031). Queensland: Moreton Bay 1(AM W5082-4), 1(AM W5066), 1(AM W7047), 1(QM G6701); Gladstone, Calliope River 1(AM W10340), 1(AM

W10341), 1(AM W13476); Townsville, Halifax Bay 1(AM W199027).

Description. Ten pairs of thoracic notopodia from segment 3. Notosetae fine, smooth, capillaries, appear very narrowly winged under high power (Fig. 1f,g) and, in some cases finely hirsute distally, perhaps as a result of wear. Achaetous region between thorax and abdomen with 3–8 segments, less than or equal to length of thorax. Abdomen of larger animals (eg. QM G6701)

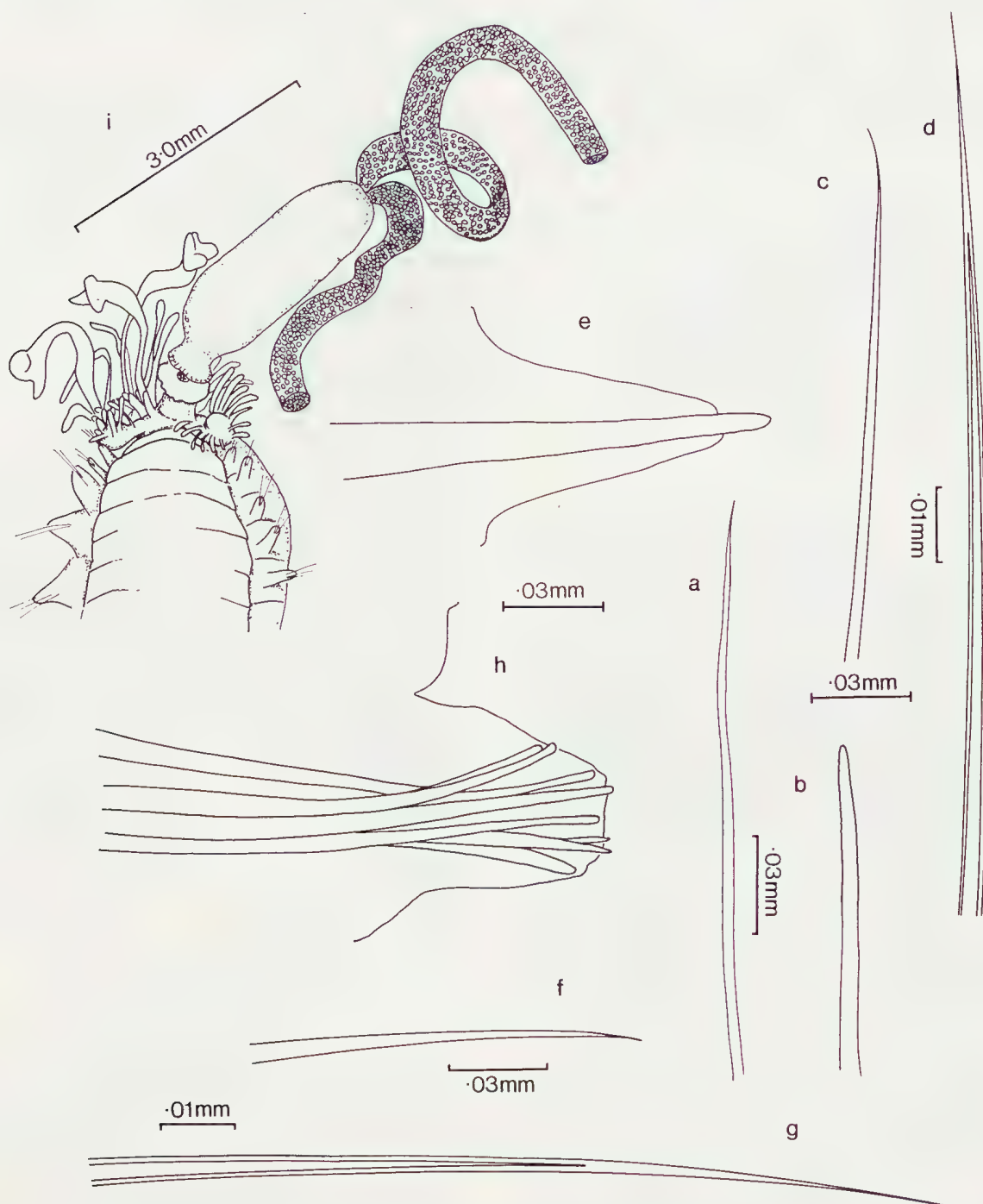


Fig. 1. *Amaeana antipoda*: a, midthoracic notoseta; b, midabdominal neuroseta. *Amaeana apheles*: c,d, midthoracic notoseta; e, midabdominal neuropodium and neuroseta. *Amaeana trilobata*: f,g, midthoracic notoseta; h, midabdominal neuropodium and neurosetae; i, head end showing reproductive structure (AM W10341).

with up to 70–80 pairs of abdominal neuropodia and 15 slender acicular spines per neurosetal fascicle (range 3–15) (Fig. 1h).

Remarks. The material examined varied more than indicated in previous descriptions with regard to the number of achaetous segments between thorax and abdomen.

Amaeana trilobata (Sars, 1863), originally described from Norway, has since been reported from around the world. Material labelled as types of *A. trilobata* has been re-examined and, although posteriorly incomplete, closely resembles the Australian material, with 10 pairs of notopodia and about five achaetous segments between the thorax and the abdomen. Prominent nephridial papillae are present on setigers 4–10 with the last two pairs being very small. The ventrum is highly papillated, and the notosetae are broad bladed, narrow winged capillaries.

A few sexually mature females (eg. AM W7047, W10341), collected in December and October respectively from Moreton Bay and Calliope River in Queensland, showed a peculiar reproductive structure. Two long, cylindrical and transparent egg tubes were attached distally to a larger, thicker walled sac which was in turn attached by a narrow neck to the tentacular membrane. A duct connected this structure with the coelom (Fig. 1i). The egg tubes in both specimens contained embryos at the 3-segment stage, and the proximal sac, which was presumably secreted later, contained embryos in the late cleavage–early blastula stage. We have seen no examples of similar structures in other terebellids, although Thorson (1946) reports *Nicolea zostericola* (Oersted) having transparent egg tubes attached to the outer surface of the female tube. The significance of this reproductive adaptation is unclear, but it is a fragile structure which would be easily dislodged by rough initial sorting. Thus it may be more widespread than our material indicates.

Habitat. Bays and marine areas of estuaries; in coarse sediment and mud, often associated with seagrass in shallower areas; intertidal to 20 m. Also from Bass Strait and off east coast of Tasmania in 40–91 m, and the North West Shelf in 40–80 m in sandy and gravelly sand sediment.

Distribution. Western Australia, South Australia, Tasmania, Victoria, New South Wales and Queensland (Fig. 12A). Arctic; Norway; North Carolina, USA; Mediterranean; Japan.

Hauchiella Levinsen

Hauchiella Levinsen, 1893: 351.

Type species. *Polycirrus tribullata* McIntosh, 1869, by monotypy.

Description. Shape of body typical of subfamily, except that all notopodia, neuropodia and setae are lacking. Tentacular membrane expanded, with 2 types of tentacles. Thorax of about 10 segments; usually about 70 segments in total.

Key to Australian species of *Hauchiella*

- Body with papillated ventral epidermis on first 10 segments; 9–15 pairs of nephridia from segments 3–6. *H. renilla*
- Body with ventrum smooth anteriorly; 4 pairs of nephridia from segment 5. *H. tribullata*

To date, only 2 species of this genus have been described.

Hauchiella renilla n. sp.

Figs 2a,b; 12B

Material examined. HOLOTYPE: Australian Capital Territory, Wreck Bay, Cemetery Point (35°10'S 150°41'E) 15 m, (AM W199607), coll. P. Hutchings, 27 Feb 1976, complete, about 52 segments, 8.5 mm long, 1.3 mm wide. PARATYPES: Queensland, One Tree Island (23°30'S 152°05'E) 10 m, 1(AM W199613), 1(AM W199614), 1(AHF Poly 1452); Lizard Island (14°40'S 141°28'E) 10 m, 1(AM W199610), 1(AM W199612), 1(AM W199611), 1(AM W199608), 1(AM W199609), 1(BMNH ZB 1985.223), 1(USNM 098818). Specimens range in width from 0.3–1.4 mm. Material examined from Lizard Island represents a selection of material available.

Description. Colour of alcohol-preserved material pale yellow, with some irregular patches of light brown pigment on tentacles and body. Body fragile, generally of uniform width, except inflated midanteriorly; posterior body with segments short, crowded. Epidermis dorsally smooth and ventrally minutely papillate on segments 2–7 (Fig. 2a). Midventral–medial groove poorly defined as 2 narrow, glandular streaks extending posteriorly from peristomium, faintly segmented anteriorly and posteriorly. Tentacular membrane expanded, weakly trilobate, with lateral lobes merely slight thickenings of basal margins of medial lobe. Tentacles with a shallow medial groove, with variable degrees of subdistal inflation (Fig. 2a).

Peristomium about 3 times length of segment 2 middorsally, slightly inflated ventrally, forming a minute, rounded lower lip. Succeeding segments without setae, acicula or podial projections. Nephridia elongate, curved sacs visible through body wall from segment 6, 10 pairs (Fig. 2a); nephridial papillae absent, pores minute and visible on some segments.

Pygidium with a small ventral papilla partially covering anus; anus terminal (Fig. 2b).

Variation. Variations not included for the holotype include: dorsal epidermis in larger specimens faintly tessellated anteriorly; ventral epidermis with papillae becoming smaller and more sparse beyond segment 10. Lower lip small, oval to crescent shaped. Nephridia first present from segments 3–6, extending to segments 12–17, present in all paratypes, thus the number of pairs of nephridia varies from 9 to 15 pairs. Nephridial pores minute, visible laterally on all nephridial segments in larger specimens. Mature females (AM W199610,

BMNH ZB 1985.223, AM W199611, AM W199609) have the body wall distended with eggs, and nephridial pores as described for the holotype.

Comments. The genus *Hauchiella* lacks setae, which are typically used to separate species within a genus of Polycirrinae, either in terms of where the setae begin,

or numbers of pairs of parapodia, and in some cases the shape or ornamentation of the setae are important specific characters. Therefore the only character which can be used as a specific character in *Hauchiella* is the number and arrangement of the nephridiopores. *Hauchiella renilla* n. sp. can be distinguished on this basis from *H. tribullata* (McIntosh, 1869), the only

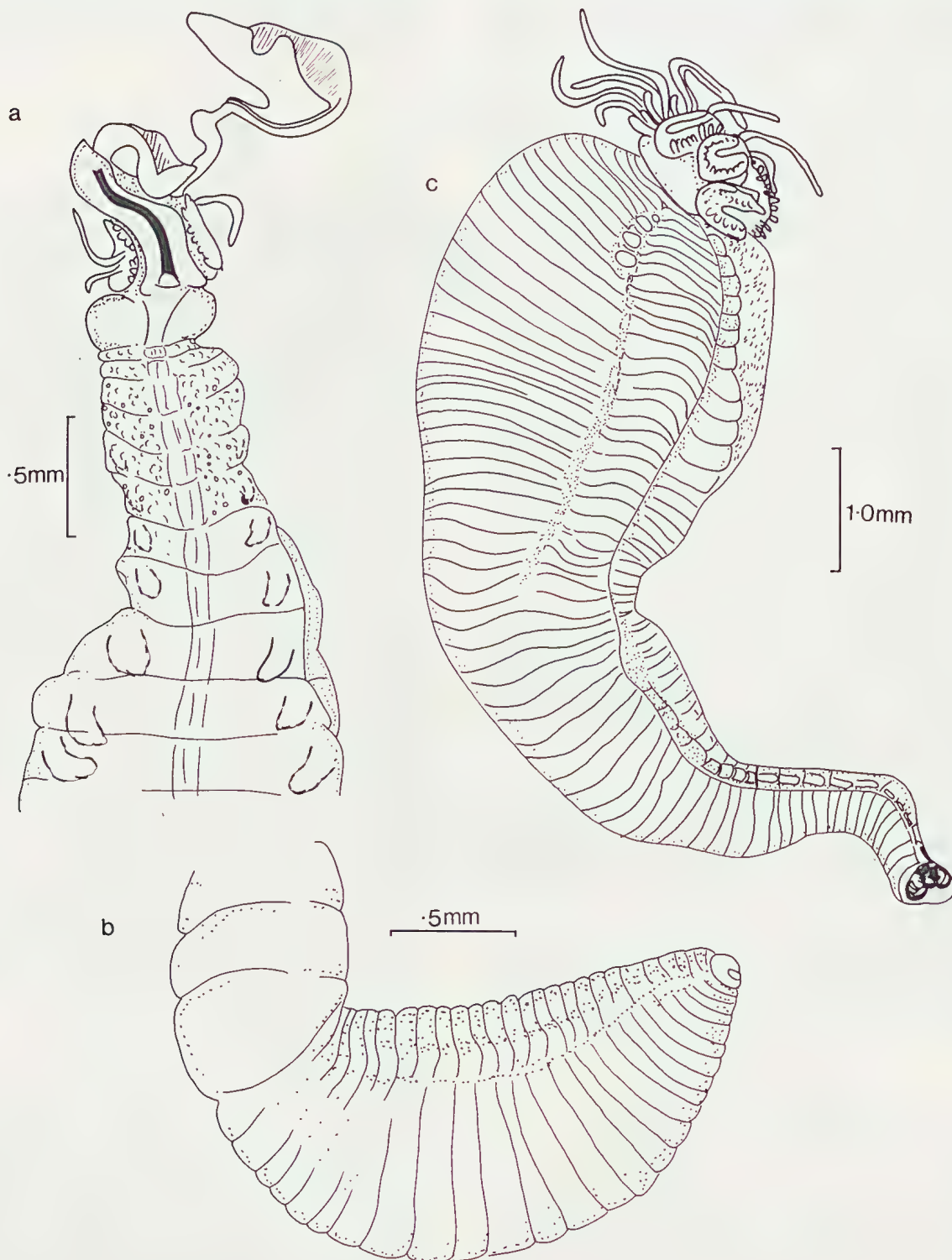


Fig. 2. *Hauchiella renilla* n. sp., holotype: a, ventral view of head end; b, ventrolateral view of tail end. *Hauchiella tribullata* (NMV F50350): c, ventrolateral view of entire animal.

other species known. *Hauchiella renilla* has 9–15 pairs of nephridia occurring from segments 3–6, whereas *H. tribullata* has four pairs of nephridia present from segment 5.

Habitat. Dead coral substrata at Lizard Island and One Tree Island, Great Barrier Reef; in coralline algae at Cemetery Point; 5–10 m.

Distribution. Australian Capital Territory and Queensland (Fig. 12B).

Etymology. Specific name derived from the Latin, *renis*, for kidney, referring to the numerous, minute nephridial pores.

Hauchiella tribullata

Figs 2c; 12B

Polycirrus tribullata McIntosh, 1869: 424.

Lysilla inermis Ehlers, 1913: 567–568, pl XLIV figs 14–16.

Hauchiella tribullata.—Hessle, 1917: 233, with synonymy; McIntosh, 1922: 201–202, pl CXXXVIII figs 13, 13a, 13b, with synonymy; Monro, 1930: 197; 1936: 184–185; Hartman, 1966: 103–105, pl. XXXV fig.1.

Material examined. Victoria: Bass Strait, Stn 183 (39°07.0'S 143°14.6'E), 84 m, 1(NMV F50350) complete, about 44 segments, 8.2 mm long, 2.9 mm wide. HOLOTYPE: (BMNH ZK 1921.5-1-4120) dredged off St Magnus Bay, Shetland, in 90 fm, muddy sand, coll. J. Gwyn Jeffreys, July 1867.

Description. Body short, fusiform, widest midanteriorly, gradually tapering abdomen. Segments biannulate throughout except for first few (Fig. 2c). Midventral groove shallow, segmented, broad anteriorly. Tentacular membrane expanded with convoluted, frilly margin. Lower lip small, pentagonal. Setae absent. Segments 5–8 each with a pair of swollen papillae laterally, probably nephridial, first pair slightly smaller. Pygidium with a pair of rounded papillae laterally; anus terminal (Fig. 2c).

Comments. The holotype is in two pieces, very damaged, and with part of the thorax removed. The Bass Strait specimen has three pairs of white glandular patches, present laterally on segments 6–8, and a pair of minute papillae on segment 5 which are probably nephridiopores and which closely resemble the holotype. For these reasons the material from Bass Strait is referred to *H. tribullata* (McIntosh, 1869). Until now, all specimens of *Hauchiella* have been referred to *H. tribullata*, and probably a selection of this material should be re-examined to confirm if this species is really as widespread as the literature suggests. In many cases, material identified as *H. tribullata* has not been deposited in a museum for subsequent verification, so it is not possible to check most records. However, when sufficient material becomes available, the number and arrangement of the nephridia should be carefully checked. It would also be helpful if additional material in good condition could be collected from the type locality to determine the range, if any, in the distribution and number of pairs of nephridia in *H. tribullata*.

Habitat. Continental shelf, 84 m in sandy shell sediment.

Distribution. Bass Strait (Fig. 12B). North-west Europe, Britain, South Georgia and off Antarctic mainland.

Lysilla Malmgren

Lysilla Malmgren, 1866: 392.

Type species. *L. loveni* Malmgren, 1866, by monotypy.

Description. Expanded tentacular membrane, trilobed, with 2 types of buccal tentacles. six to 12 thoracic segments, notopodia from segment 3; notosetae either smooth, hirsute or pinnate capillaries. Neurosetae completely absent.

Key to Australian species of *Lysilla*

1. Tentacular membrane posterodorsally fringed; notosetae hirsute capillaries. *L. laciniata*
- Tentacular membrane posterodorsally smooth; notosetae smooth or pinnate capillaries. 2
2. Lower lip bilobed; 8–10 pairs of notopodia, notosetae pinnate. *L. bilobata*
- Lower lip not bilobed; 8–13 pairs of notopodia, notosetae pinnate or smooth. 3
3. 8–10 pairs of notopodia, notosetae smooth. *L. jennacubinae*
- 11–13 pairs of notopodia, notosetae pinnate. *L. pacifica*

Lysilla bilobata n. sp.

Figs 3a–d; 4a,b; 12C

Lysilla pacifica.—Hutchings, 1974: 191 (in part); 1977: 11. Not Hessle.

Material examined. HOLOTYPE: New South Wales, Stn 81, Woollooware Bay, Georges River (33°05'S 151°06'E), (AM W7586), coll. L. Collett, NSWSE, posteriorly incomplete, about 40 segments, 15.5 mm long, 2.0 mm wide. PARATYPES: New South Wales, Wallis Lake (32°17'S 152°29'E), 1(BMNH ZB 1985.224), 1(AHF Poly 1453); Woollooware Bay, Georges River 2(AM W199531); Botany Bay (33°06'S 150°59'E), 3(AM W195770), 7(AM W18947), 1(AM W195466), 1(AM W13973); Avoca Reef (33°28'S 151°26'E), 1(USNM 098819); Port Stephens (32°37'S 152°04'E), 2(AM W12429). Paratypes range in width from 1.0–2.2 mm.

Additional material examined. Western Australia: North West Shelf off Port Hedland 2(AM W199530), 1(AM W199522), 1(AM W199524); Mermaid Sound, Dampier Archipelago 1(WAM 18-84); 8 km north-west of Dongara 1(WAM 40-84). South Australia: Karatta Beach, Robe 1(AM W199515). Victoria: Bass Strait, Stn 81 (39°28'S 143°17'E) 103 m, 1(NMV F50349). Queensland: Nerang River, Gold

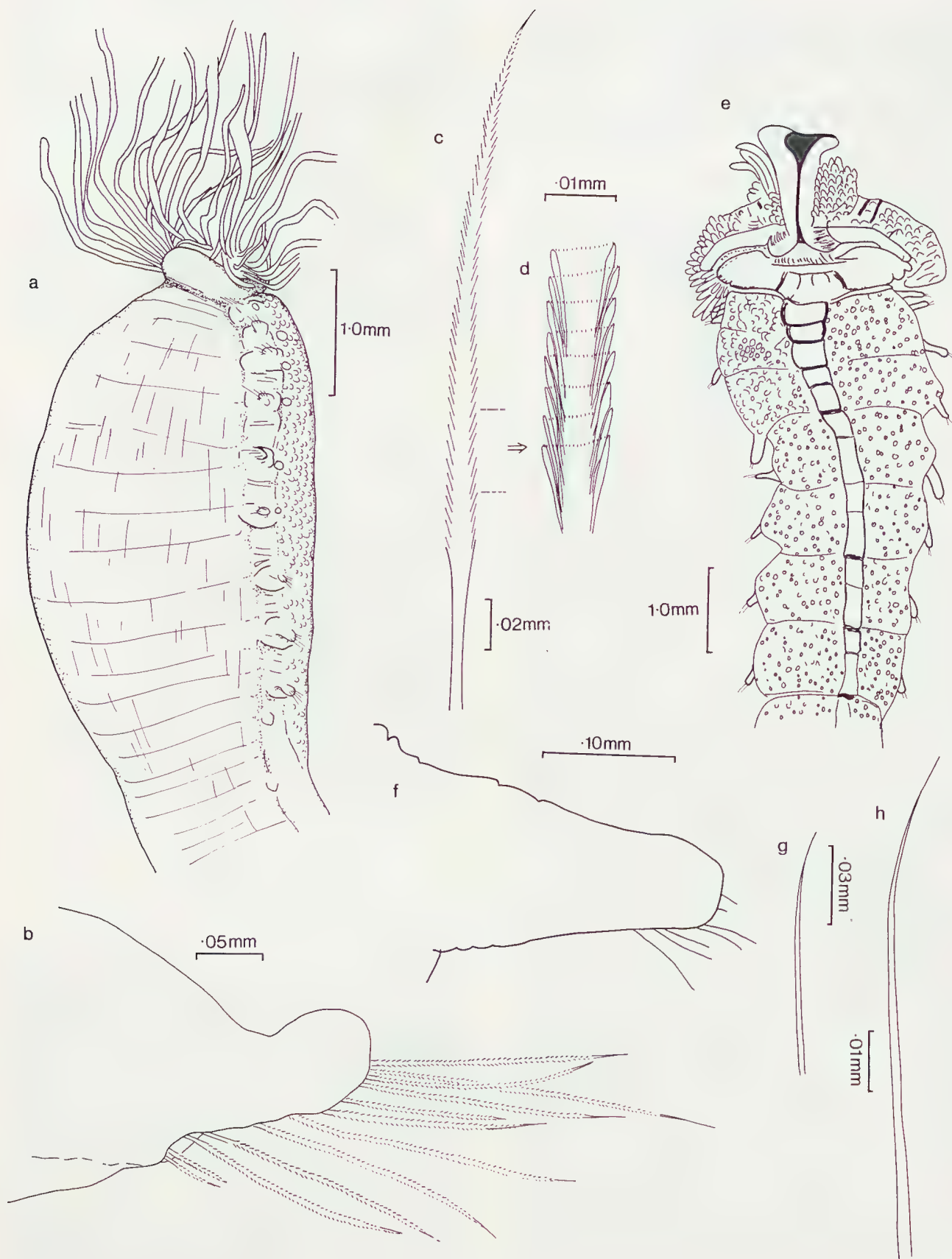


Fig. 3. *Lysilla bilobata* n. sp., holotype: **a**, lateral view of head end; **b**, anterior view of notopodium 2, left side. *Lysilla jennacubinae* n. sp., holotype: **c,d**, notoseta; **e**, ventral view of head end; **f**, anterior view of notopodium 5, left side; **g,h**, notoseta from same.

Coast 1(AM W10870); Moreton Bay several(AM W7040-4); Gladstone, Auckland River 1(AM W10330), 2(AM W13185), 1(AM W13287), 1(AM W13479); Calliope River 1(AM W8520), 1(AM W10337), 1(AM W13479).

Description. Body fragile, thorax and posterior abdomen inflated slightly. Segments faintly annulated anterodorsally, annulations more distinct on posterior abdomen, 3-4 per segment. Thoracic epidermis faintly tessellated dorsally, densely papillated ventrally; first 3 setigers with very large papillations medially (Fig. 3a). Midventral groove shallow, divided into many short, smooth glandular pads on thorax and abdomen. Tentacular membrane trilobed, medial lobe with a deep longitudinal cleft dorsally, lateral lobes much smaller than medial lobe. Tentacles long, grooved, thickness variable, subdistally expanded, densely intertwined. Peristomium obscured dorsally, forms a bilobed lower lip ventrally, with grooved lobes projecting anteroventrally.

Segment 2 achaetous, about 0.5 times width of segment 3 dorsally and laterally, partially obscured ventrally due to contracted state of animal. Notopodia from segment 3, 9 pairs; short, similar length throughout, distally with a long, globular presetal lobe and shorter, triangular postsetal lobe (Fig. 3b). Segments 12-14 each with a pair of low rounded papillae in place of notopodia (Fig. 3a). Notoetae short, relatively stout, capillaries; shafts emerging from notopodia smooth, nearly 0.5 times width of proximal ornamented region (Fig. 3c,d). A scanning electron microscope photograph of one specimen shows the bilobed lower lip and capillaries with whorls of spines along the tip (Fig. 4a,b).

Nephridial papillae small, at ventral base of notopodia of setigers 1-6 (Fig. 3a); nephridial pore only at base of notopodia 7-9.

Variation. The paratypes and additional material examined exhibit the following variation: number of notopodia ranged from 8-10 pairs; in some smaller specimens nephridial papillae are absent, in the larger specimens 3 pairs of large gonopores are present on setigers 4-6 at the ventral base of the notopodia, in place of the nephridial papillae.

Comments. *Lysilla bilobata* was not differentiated from *L. pacifica* Hesse by Hutchings, 1974, who described material of both species from Wallis Lake as belonging to *L. pacifica*, with 9-13 pairs of notopodia.

Lysilla bilobata is smaller than *L. pacifica*. It has: a bilobed lower lip; 8-10 pairs of short notopodia with notosetae with whorls of spines along the tip, and with markedly thinner shafts than *L. pacifica*; some larger specimens have three pairs of large gonopores at the base of notopodia on setigers 4-6. *Lysilla pacifica* has a small semi-circular, dome shaped lower lip, 11-13 pairs of elongate notopodia, notosetae with slightly less coarsely spined capillaries and thicker shafts than those of *L. bilobata*. On the larger specimens of *L. pacifica*, elongate nephridial papillae occur at the base of each notopodium.

Both *L. bilobata* and *L. pacifica* are recorded from Botany Bay, Wallis Lake and Port Stephens. In these areas, they appear to occupy similar niches, in association with seagrasses in muddy sand sediment. In Wallis Lake, the two species have been collected in the same samples. *Lysilla bilobata* is the more widespread of the two species in Australian waters, occurring offshore in Bass Strait and off Port Hedland, Western Australia, in 40-80 m, as well as in shallow coastal waters on the east coast.

Habitat. River mouths, sheltered bays, continental shelf, 4-80 m, mud to coarse sand, associated with the seagrasses *Zostera* and *Posidonia* in shallow waters.

Distribution. Western Australia, South Australia, Bass Strait, New South Wales and Queensland (Fig. 12C).

Etymology. The specific name *bilobata* is derived from the Latin *bi* and *lobus*, an elongated projection or protruberance, referring to the peculiar double lobed lower lip of the peristomium.

Lysilla jennacubinae n. sp.

Figs 3e-h; 12c

Material examined. HOLOTYPE: Queensland, Caloundra (26°48'S 153°08'E), (AM W199643), coll. I. Loch, 20 Oct 1976; complete, about 84 segments, 21 mm long, 2.0 mm wide. PARATYPE: New South Wales, Woolgoolga (30°07'S 153°21'E), (AM W199644), coll. F. Rost, 5 Nov. 1963; complete, 2 fragments, about 93 segments total, 21 mm long, 1.2 mm wide.

Description. Body coiled, widest at anterior abdomen, posterior abdomen slightly inflated; abdomen long with numerous very short segments. Colour in alcohol reddish brown. Dorsal epidermis faintly tessellated with weak transverse grooves, 5-7 per segment anteriorly, number increasing up to 15 per segment on posterior thorax to midabdomen, reducing to 2-5 per segment on posterior abdomen. Ventral thoracic epidermis coarsely papillated; midventral groove smooth, shallow, divided into distinct glandular pads to pygidium (Fig. 3e). Tentacular membrane trilobed, lobes approximately equal in size, laterally extending almost to tip of anterior notopodia. Buccal tentacles largely missing. Peristomium approximately twice the width of segment 2 dorsally, reduced laterally, ventrally smooth, slightly inflated with a thin, broad, longitudinally grooved lower lip.

Segment 2 achaetous, reduced laterally and ventrolaterally; ventrally forms a large glandular pad projecting anteriorly into peristomial segment. Notopodia from segment 3, 10 pairs, last pair papilliform, without notosetae; notopodial lobes elongate, some distally recurved, reducing in length after first few (Fig. 3f). Notoetae few, slender, smooth, wingless capillaries, present in graded lengths (Fig. 3g,h).

Nephridial papillae present on anterior base of

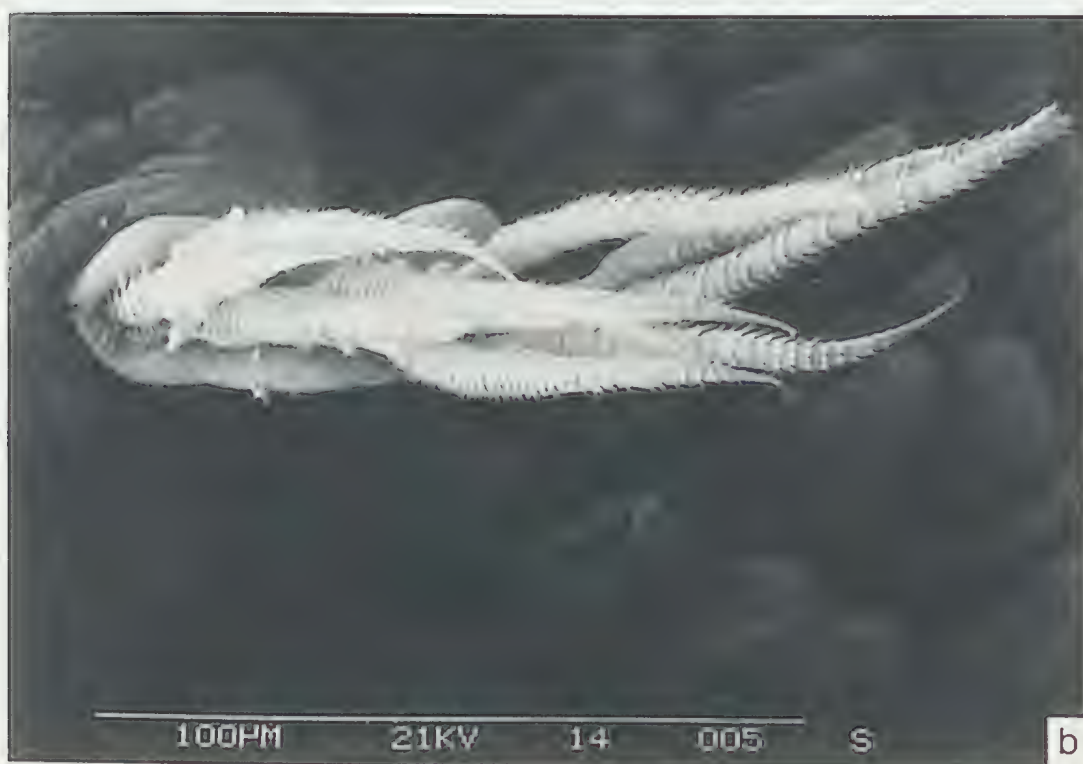


Fig. 4. *Lysilla bilobata* n. sp.: a, S.E.M. ventral view of head end; b, notopodial fascicle showing emergent notosetae, S.E.M. photograph.

notopodia on segments 6–12 and in equivalent position on next 3–5 segments which lack notopodia; increasing in size from minute papilliform projections initially to large, globular processes on segments 14 and 15. Pygidium with a rounded ventral papilla; anus terminal.

Variation. The paratype showed the following variations. Posterior abdomen with a shallow, middorsal groove; tentacular lobe with lateral lobes slightly longer than medial lobe; buccal tentacles with a deep medial groove, faintly annulated. Notopodia from segment 3, continuing for 8 pairs. Nephridial papillae on the anteroventral base of notopodia on segments 3–9; on segments 9–10 large white glandular swellings ventral to notopodia, perhaps gonopores although no pore visible.

Comments. *Lysilla jennacubinae* is described as a new species as it differs from the other described species of *Lysilla* in having 8–10 pairs of notopodia with smooth capillary setae. The other species of *Lysilla* with smooth setae (*L. alba* Webster, 1879, *L. loveni* Malmgren, 1865, *L. loveni macintoshi* Gravier, 1907 and *L. pambanensis* Fauvel, 1928) can be distinguished from *L. jennacubinae* by the number of pairs of notopodia. *Lysilla loveni* and *Lysilla loveni macintoshi* both have a maximum of six pairs of notopodia, and *Lysilla pambanensis* Fauvel has 13–18 pairs of thoracic notopodia.

Lysilla alba Webster apparently has very few pairs of notopodia according to Webster who found only one fascicle amongst the syntypes. He figures a seta which differed from *L. jennacubinae* in having well developed lateral wings which appear finely striated, although smooth in outline. In our examination of the syntypes of *L. alba* (USNM 435) from Virginia, USA, we found no trace of any setae or notopodia, although some specimens had large sections of the thorax removed. Clearly more animals of this species need to be examined to ascertain whether it belongs to *Lysilla* or perhaps the asetigerous genus *Hauchiella*.

Habitat. Rock pools on platforms of exposed rocky headlands.

Distribution. New South Wales and Queensland (Fig. 12C).

Etymology. The specific name *jennacubine* is derived from a Western Australian aboriginal tribal name for a salt water pool.

Lysilla laciniata n. sp.

Figs 5a–e; 12C

Material examined. HOLOTYPE: (AM W199626), complete, about 80 segments, 43 mm long, 3.4 mm wide, sexually mature female. PARATYPES: 10(AM W199627), 1(AHF Poly 1454), 1(BMNH ZB 1985.225), 1(USNM 098820), range in size from about 55 segments, 22 mm long and 1.4 mm wide to about 69 segments, 53 mm long and 4.0 mm wide. All types from South Australia, Coffin Bay (34°28'S 135°19'E), coll. I. Thomas, 1 Dec 1978.

Description. Body large, tapering gradually posteriorly from an inflated anterior thorax. Dorsal

epidermis smooth anteriorly and on midbody segments, with a posteriorly broad transverse band of minute papillae on each segment. Ventral epidermis heavily papillated on anterior thorax, faintly papillated on remaining thorax, smooth thereafter; midventral groove shallow, with smooth glandular segments extending from posterior thorax to pygidium (Fig. 5b). Tentacular membrane trilobate, lobes approximately equal in size; posterodorsal edge fringed, forming 2 lappets, just extending over anterior edge of peristomium (Fig. 5a). Buccal tentacles consisting of 2 types: thin, slightly subdistally expanded; and longer, greatly subdistally expanded types; both types of tentacles shallowly grooved distally. Peristomium about equal in length to segment 2 dorsally, ventrally forms a semispheroidal lower lip, which is longitudinally grooved.

Segment 2 achaetous, very short, ventrally projects slightly into peristomium. Notopodia from segment 3, continuing for 10 pairs; notopodia short, distally blunt, slightly recurved dorsally (Fig. 5c), approximately equal lengths throughout. Notosetae few, slender, hirsute capillaries (Fig. 5d,e), arranged in graded lengths.

Nephridial papillae small, present at anteroventral base of all notopodia, emerge from centre of a small, white glandular swelling. Posteroventral surface of pygidium with a rounded papilla; anus terminal.

Variation. Paratype material closely resembles the holotype. Variations not included in the description of holotype include the following: thorax of some small specimens are not anteriorly inflated; posterodorsal edge of tentacular segment with fringe forming 2–5, ill-defined lappets ranging in size from a slight thickening to lappets which extend over anterior portion of peristomium; notopodia from segments 3, 9–11 pairs; 1 paratype (AHF) with 1 reduced notopodium, slightly dorsally displaced, on left side of segment 2. All paratypes with small nephridial papillae at base of notopodia, smaller specimens without associated glandular swelling.

Comments. *Lysilla laciniata* is described as a new species because of the unique development of the fringe on the tentacular membrane. No such structure has been described from any of the other described species and one subspecies of *Lysilla*. The only other species of *Lysilla* having hirsute notosetae, *L. albomaculata* Caullery, 1944, appears to be similar to *L. laciniata* in general body shape and in the number of pairs of notopodia (12), although this species appears to have a smooth ventral epidermis and no nephridial papillae on the first three setigers although they are present on setigers thereafter, and this species has only been recorded from abyssal depths off Indonesia. Caullery also does not mention any fringe on the tentacular membrane.

Habitat. Amongst the roots of the seagrass *Zostera* at low tide levels.

Distribution. South Australia (Fig. 12C).

Etymology. Specific name derived from the latin, *lacinia* (feminine), meaning fringe or lappet on the

border of a garment, referring to the peculiar fringe on the posterodorsal edge of the tentacular membrane.

Lysilla pacifica

Figs 5f-i; 12C

Lysilla pacifica Hessle, 1917: 232-233, fig. 66.—Okuda, 1940: 22; Imajima & Hartman, 1964: 348; Hutchings, 1974: 191 (in part); Hutchings & Rainer, 1979: 786; Hutchings & Murray, 1984: 90-91.

Lysilla ubianensis Caullery, 1944: 197, fig. 156a-e.—Day, 1957: 114; 1967: 721, fig. 36.3i-j.

(?)*Polycirrus boholensis*.—Rullier, 1965: 196. Not Grube.

Material examined. New South Wales: Jervis Bay 1(AM W5219); Port Hacking, Maianbar 1(AM W11044); Botany Bay 6(AM W12290), 1(AM W194917), 2(AM W12360); Careel Bay 2(AM W5745), 2(AM W5771), 1(AM W10505), 1(AM W10508); Cowan Creek 1(AM W196784); Lake Macquarie 1(AM W17845); Port Stephens, Myall River 1(AM W6129); Broughton Island 1(AM W13062); Wallis Lake many(AM W4209), 1(AM W5136). Queensland: Stradbroke Island, Dunwich 1(QM G3606); Hervey Bay 1(AM W5349).

Japan: 1(UZM nr. 181a), 1(UZM nr 181b), Misaki; 1(UZM nr 181c) Port Lloyd, Bonin Islands (Ogasawara-guntō); all SYNTYPES, collected by Dr Sixten Bocks, Japan Expedition, 1914.

Comments. The Australian material examined appears almost identical to the syntypes of *Lysilla pacifica*, collected from Japanese waters. Australian specimens are slightly larger and have 11-13 pairs of notopodia whereas the syntypes have 10-11 pairs of notopodia (Fig. 5f,g). The notosetae are pinnate capillaries arranged in graded lengths along the ventral side of the notopodia (Fig. 5h,i). In the type description, Hessle states that there are 9-12 pairs of notopodia and that this variation may occur between the left and right sides in the one individual. Such a variation in number of pairs of notopodia within an animal was not observed in our Australian material. The number of pairs of notopodia, however, did appear to increase with body size, although no animals were observed with less than 11 pairs of notopodia. One previous description of *Lysilla pacifica* (Hutchings, 1974) stated that as few as 9 pairs of notopodia may be present. However in these cases the two species *L. pacifica* and *L. bilobata* were confused.

The holotype of *Lysilla ubianensis* Caullery, 1944, from the Philippines (ZMA V.pol 1537) was also examined and would appear to be synonymous with *L. pacifica* (see Hutchings, 1974). The holotype is posteriorly incomplete, with about 26 segments, 13 mm long, 1.8 mm wide and characterised by having a densely papillated thoracic ventrum, a small dome shaped lower lip, 11 pairs of notopodia with slender, pinnate, capillaries and large nephridial papillae on the anteroventral base of notopodia on segments 3-14, which falls within the variation exhibited by *L. pacifica*.

One specimen from Dunwich, Queensland (QM G3606), tentatively identified by Rullier (1965) as *Polycirrus boholensis* Grube, was re-examined and is

referred to *Lysilla pacifica*.

Habitat. Coastal lagoons, sheltered bays and estuaries in shallow mud-sandy areas often associated with the seagrasses *Zostera* and *Posidonia*.

Distribution. New South Wales (widespread) and Queensland (Fig. 12C). Japan, Philippines, South Africa and Solomon Islands.

Polycirrus Grube, emended

Aphlebina Quatrefages in Milne Edwards, 1844: 18.

Torquea Leidy, 1855: 146.

Apneuma Quatrefages, 1865: 380.

Leucariste Malmgren, 1866: 390.

Ereutho Malmgren, 1866: 391.

Cyaxares Kinberg, 1866: 348.

Dejoces Kinberg, 1867: 348.

Anisocirrus Gravier, 1905: 437.

Litancyra Hutchings, 1977: 10.

Type species. *P. medusa* Grube, 1850, by monotypy.

Description. Expanded tentacular membrane trilobate, sometimes with lateral lobes reduced, with 2 types of buccal tentacles. Thorax with a variable number of setigers, notopodia from segment 2 or 3. Neuropodia first present from segments 7-18. Notoetae variable; include pinnate, hirsute, smooth winged or smooth wingless capillaries, but only 1 or 2 types of setae present in any one species.

Comments. The generic diagnosis is expanded to include the form of the tentacular membrane. The tentacular region, derived from the prostomium, is expanded anteriorly along the medial axis and laterally to form a trilobate membrane. The degree of lateral and medial expansion is variable. Tentacles are attached along the distal margin of the membrane, which is often convoluted. The upper lip is fused fully or partially with the ventral surface of the tentacular membrane or may remain free. Posteriorly, the tentacular membrane is thickened as a ridge dorsally and laterally. The peristomium is visible dorsally and is about the same length of segment 2 middorsally, but usually the peristomium is absent laterally and ventrally. The ventral lower lip, which varies in its development, is derived from the peristomium.

The type species of *Polycirrus*, *P. medusa*, has notopodia beginning on segment 3. Since the genus was erected, other species with notopodia beginning on segment 2 have been included: *P. albicans* (Malmgren, 1866), *P. arenivorus* Caullery, 1915, *P. aurantiacus* Grube, 1860, *P. caliendrum* Claparède, 1878, *P. carolinensis* Day, 1973, *P. denticulatus* Saint-Joseph, 1894, *P. eximius dubius* Day, 1973, *P. haematodes* (Claparède, 1864), *P. hamiltoni* Benham, 1921, *P. hesslei* Monro, 1930, *P. latidens* Eliason, 1962, *P. pallidus* (Claparède, 1864) and *P. plumosus* (Wolfebaek, 1912). However the generic definition was never formally expanded to include this variation. Only two species described from Australia, *P. broomensis* Hartmann-Schröder, 1979, and *P. nephrosus* n. sp.,



Fig. 5. *Lysilla laciniata* n. sp., holotype: **a**, dorsal view of head end; **b**, ventral view of head end; **c**, anterior view of notopodium 5, left side; **d,e**, notoseta from same. *Lysilla pacifica* (AM W194917): **f**, ventral view of head end; **g**, anterior view of notopodium 9, left side; **h,i**, notoseta from same.

have notopodia present from segment 2, although there are problems in interpreting the numbering of anterior segments in these particular species. In most species of *Polycirrus* the numbering of segments can be clearly determined by examining the animal dorsally, but in the two above species anterior segmentation on the dorsal surface is obscure. We have expanded the definition of *Polycirrus* to include species with notopodia beginning on segment 2 or 3. Finally, we have included in the generic description the variety of notosetae which may occur within the genus.

Until this study, the genus *Polycirrus* contained 39 species (Fauchald, 1977), and since then an additional two species, *P. broomensis* Hartmann-Schröder and *P. rosea* Hutchings & Murray, 1984, have been described. Examining many of these species, together with the seven new species and one new combination described in this paper, has enabled us to evaluate the relative importance of the specific characters which have been used to distinguish between species of *Polycirrus*. The most important specific characters are as follows: (a) Numbers of pairs of notopodia, although only gross differences are of diagnostic value. The absolute number of pairs of notopodia tends to decrease with increasing body size. (b) First segment on which the uncini appear, but it is necessary to give the range over which this occurs for the species. The absolute number of uncini per row tends to increase with increasing body size. (c) Degree of epidermal papillations or tessellations. (d) The degree of segmentation and approximate numbers of ventrolateral glandular pads, although these may vary somewhat with increasing size of animal. (e) Form of notosetae. (f) Form of uncini, and the range of dental formulae present.

Banse (1980) used characters a,d,e,f, to separate species of *Polycirrus* and suggested that the form of the

notopodia was also important. The form of the notopodia is a highly variable character even within an individual: the pre- and postdistal setal lobes may be retracted or extended depending on the state of preservation and therefore we do not regard it as a very useful character. Banse also suggested that the dentition of the uncini as seen from a frontal view is useful in differentiating species. We have also used this character, however we stress that, as the dentition of the uncini is highly variable in some species, the dental formula should give the range, or a number of frontal views of uncini should be illustrated within a species. Finally, Banse also considered the number of pairs of nephridia to be an important specific character. We use this character cautiously as it depends on the size and or sexual maturity of the animal, which should be taken into account when describing a new species.

Many of the species currently described in the genus *Polycirrus* are inadequately described, and details such as the types of notosetae present, the dental formulae of uncini and the range over which notopodia and neuropodia occur are often not included in this description. A full revision of the genus *Polycirrus* was beyond the scope of this study, however we did examine, wherever possible, type material of species recorded from the general vicinity of the South Pacific and South East Asia. Thus our comments on the similarity of a new species to previously described species are mainly restricted to those other species occurring in the vicinity of Australasia.

The key below is an artificial key, and we have used the structure of the notosetae for convenience. We suggest that users refer to the diagrams of the setae drawn for each species to ensure the correct interpretation of our notosetal terminology.

Key to Australian species of *Polycirrus*

1. Notosetae include some ornamented capillaries (under 40x objective). 2
 —Notosetae smooth-winged capillaries (under 40x objective). 8
2. 14 or more pairs of notopodia. 3
 —9–12 pairs of notopodia. 5
3. 2 types of notosetae in each fascicle, pinnate and smooth; small species. . . *P. bicrinalis*
 —1 type of notosetae in each fascicle, pinnate (or whorled spination) or
 hirsute; large species. 4
4. Hirsute notosetae only; some thoracic segments with 2 pairs nephridial
 papillae. *P. nephrosus*
 —Pinnate (whorled spination) notosetae only; thoracic segments each with 1
 pair nephridial papillae. *P. aquila**
5. Neuropodia from segment 5–7. *P. porcata*
 —Neuropodia from segment 10–15. 6

6. Notoetae mixed – pinnate (whorled spination) and hirsute – in each fascicle.
..... *P. broomensis*
——Notoetae of single type within a fascicle. 7
7. Notoetae include pinnate (whorled spination) type in first few fascicles, then
hirsute types in mid and posterior fascicles. *P. disjunctus*
——All notoetae pinnate (whorled spination) only. *P. boholensis*
8. 8–9 pairs of notopodia; uncini with few teeth surmounting main fang. 9
——More than 9 pairs of notopodia; uncini with many teeth surmounting main
fang. 10
9. Uncini with teeth surmounting main fang, arranged in a vertical series.
..... *P. octoseta*
——Uncini with teeth surmounting main fang, arranged in a tranverse series.
..... *P. paucidens*
10. Glandular ventrolateral pads on first 5–7 setigers; ventrum essentially smooth. 11
——Glandular ventrolateral pads absent or present on first 6–13 setigers; ventrum
with obvious irregular papillations or tessellations laterally. 12
11. Uncini from segment 10, maximum of 8–10 uncini per neuropodium. *P. rosea*
——Uncini from segment 12–18, maximum of 15–30 uncini per neuropodium. ... *P. parvus*
12. Uncini from segment 15–19; uncinus with 1–2 rows of teeth surmounting
main fang. *P. variabilis*
——Uncini from segment 10–16; uncinus with 3 rows of teeth surmounting main
fang. *P. tessellatus*

* *Polycirrus aquila* Caullery, 1944, has been included in the key as it seems likely that it will be found in northern Australia.

Polycirrus aquila (Caullery)

Polycirrus (Ereutho) aquila Caullery, 1944: 192, fig. 152a–d.

Material examined. HOLOTYPE (ZMA V. pol 1532), Banda, Siboga Expedition Stn 240 (1936), 9–36 m; complete, about 68 segments, 19.1 mm long, 2.5 mm wide, mature male.

Description. Body with inflated thorax, short, tapering abdomen; first 8 setigers and abdomen with short, crowded segments. Epidermis dorsally smooth except for faint transverse grooves, ventrally lightly papillated on setigers 1–6, ventrolateral pads only slightly raised, barely discernable on setigers 1–6. Tentacular membrane small, distinctly trilobed with lateral lobes recurved anteriorly and extending to just short of tips of notopodia. Upper lip free from tentacular membrane. Midventral groove shallow on setigers 1–8, deeper thereafter. Peristomium about ½ length of segment 2 dorsally, absent laterally, forms an elongate, tongue-like projection.

Segment 2 achaetous, visible dorsally, laterally and ventrally. Notopodia from segment 3, 16 pairs. Notopodia slim, short processes, distally without pre- or postsetal lobes; last few notopodia slightly shorter. Notoetae pinnate capillaries as figured by Caullery (1944). Uncini from segment 16 occur on short rectangular lamellae; lamellae increase in size over first

few uncinigerous segments, then remain relatively constant in size up to the pygidium. Uncini with a long neck and broad, concave base as figured by Caullery (1944); dental formula MF: 3. Uncini occur in short rows, with about 10 per row in midabdominal neuropodia.

Nephridial papillae small, present on the anterior base of the notopodia on setigers 2–16.

Comments. *Polycirrus aquila* is redescribed here as the original description is inadequate and as it seems likely that the species will be found in northern Australia, at least in offshore waters. Other species of terebellids occur in both regions.

Habitat. Sediment, 9–36 m.

Distribution. Malay Archipelago. Currently only known from the type locality.

Polycirrus bicrinalis n. sp.

Figs 6a–f; 12D

Material examined. HOLOTYPE: Queensland, Lizard Island, 14°40'S 141°28'E, (AM W199637); complete with about 72 segments, 5.1 mm long, 0.5 mm wide. PARATYPES: Lizard Island 2(AM W199640), 1(AHF Poly 1455), 1(BMNH ZB 1985.226), 1(USNM 098821); Western Australia, North West Shelf, off Port Hedland, 20°23'S 118°37'E, 1(AM W199638),

1(AM W199639). One complete paratype (USNM 098821) about 85 segments, 10.5 mm long, 0.6 mm wide. Others range in width from 0.4–0.9 mm.

Description. Body filiform, coiled, uniformly wide throughout, tapering over last few segments; abdominal segments very short. Epidermis faintly tessellated on anterior dorsum, ventrally with large, rounded, glandular protruberances on setigers 1–7 then minute papillae on next few segments. Ventrolateral pads absent (Fig. 6a). Midventral glandular streak shallow, extends from setiger 8 to pygidium. Tentacular membrane expanded anteriorly along medial axis, lateral lobes reduced. Upper lip fused with tentacular membrane. Peristomium an incomplete ring, difficult to discern dorsally, forms a large, oval shaped longitudinally grooved lower lip ventrally (Fig. 6a).

Segment 2 achaetous, reduced dorsally, just visible laterally and ventrally as a thin wedge. Notopodia from segment 3, 16 pairs; notopodia short, slender with an elongate, digitiform postsetal lobe (Fig. 6b); all notopodia similar in size. Notoetae arranged in 2 tiers; 6–7 long, winged capillaries with blades appearing minutely striated under 100x (Fig. 6c), and 6–9 shorter, pinnate capillaries (Fig. 6d). Neuropodia minute rectangular lamellae present from about first abdominal segment (segment 19), and then continuing to pygidium. Uncini arranged in single, curved rows with up to 15 per row. Uncini with a broad, flat base and short, thick neck (Fig. 6e), dental formula consistent for uncini from all setigers, MF: 1:7–9 with distal most row arranged in an arc above a larger tooth (Fig. 6f).

Nephridial papillae absent. Pygidium with anus terminal.

Variation. Paratypes with body filiform, usually straight rather than coiled, ventrum of first 7–8 setigers with glandular protuberances, thereafter papillations minute. Notopodia extend for 14–16 segments. Uncini from near first abdominal segment (segment 17–20), increase up to 15–25 per row; dental formula consistent within an individual but varying between individuals from MF: 1:5–9 to MF: 1:7–10. Nephridial papillae absent.

Comments. *Polycirrus bicrinalis* most closely resembles *P. broomensis* Hartmann-Schröder, 1979, *P. plumosus* (Wolfebaek, 1912) and *P. hamiltoni* Benham, 1921. It differs from *P. broomensis* in the number of pairs of notopodia, the type of notosetae and the segment on which the neurosetae begin (see Table 1). *Polycirrus hamiltoni* has notopodia from segment 2, on a specimen from the type locality (AM W824) which is probably the holotype, and they continue over most of the body length whereas in *P. bicrinalis* only 14–16 pairs of notopodia are present. *Polycirrus plumosus*, described from Norway, has similar notosetae to *P. bicrinalis* but the notopodia begin on segment 2 rather than on segment 3. In addition the structure of the tentacular lobe is tripartite in *P. plumosus* whereas in *P. bicrinalis* it is expanded anteriorly along the medial axis with lateral lobes reduced.

Polycirrus bicrinalis can be distinguished from other species of *Polycirrus* occurring in Australia (Table 1).

Habitat. Coral substrata at Lizard Island, and muddy sediments in 40–80 m on North West Shelf.

Distribution. Western Australia and Queensland (Fig. 12D).

Etymology. The specific name *bicrinalis* is derived from the latin for two, *bi*, and for hair, *crinis* (masculine), referring to the two types of setae occurring in each notopodial fascicle.

Polycirrus bohollensis

Figs 6g–l; 12F

Polycirrus bohollensis Grube, 1878: 242–243, pl. XIII fig.7.

Material examined. HOLOTYPE (ZMB 10654), Bohol, Philippines, coll. Grube; fragmented, in poor condition, total length about 11.9 mm for 46 segments, maximum width about 1.8 mm. Queensland: One Tree Island, 23°30'S 152°05'E, 1(AM W199624), 1(AM W199625), 1(AM W199532); Lizard Island, 14°40'S 141°28'E, 1(AM W199533), 3(AM W199537), 1(AM W199535), 2(AM W199534), 1(AM W199623), 2(AM W199536). Specimens range in size from 27 segments, 8.3 mm long, 1.8 mm wide to 57 segments, about 18 mm long, 2.2 mm wide.

Description. Body coiled, widest anteriorly, gradually tapering over abdomen; a deep midventral groove present throughout. Epidermis smooth on dorsum, a few low papillae present on lateral ventrum (Fig. 6g). Ventrolateral pads indistinct. Tentacular membrane trilobed, each lobe approximately equal in size. Upper lip distally free from tentacular membrane, peristomium an incomplete ring, just less than length of segment 2 dorsally, absent ventrally, and forming a small, posteriorly recurved lower lip (Fig. 6g).

Segment 2 achaetous, reduced laterally, absent ventrally. Notopodia from segment 3, 10–11 pairs; notopodia elongate slightly tapered, occasionally with a small rounded supraseta lobe (Fig. 6h). Notoetae apparently pinnate under 40x objective, consisting of a stack of inverted cones nestled one on top of the other (Fig. 6i,j). Neuropodia, rectangular lamellae from segment 13–15; lamellae slightly elevated from body wall initially, increasing in length over next few segments then remaining at same degree of elevation to pygidium. Uncini with a concave base and long narrow neck (Fig. 6k); dental formula MF: 1:3–12 (Fig. 6l). Uncini arranged in single, short rows throughout, maximum of 7–10 per neuropodial row.

Nephridial papillae present on setigers 1–11 or setigers 2–11 at anterior base of notopodia, absent in small specimens. Pygidium with a low, rounded papillae on ventral margin; anus terminal.

Comments. We have expanded Grube's description of the species and put a greater emphasis on characters we consider important (p.330). This species may be distinguished from other species of *Polycirrus* in having pinnate notosetae, uncini with a very long secondary tooth surmounting the main fang and a variable number

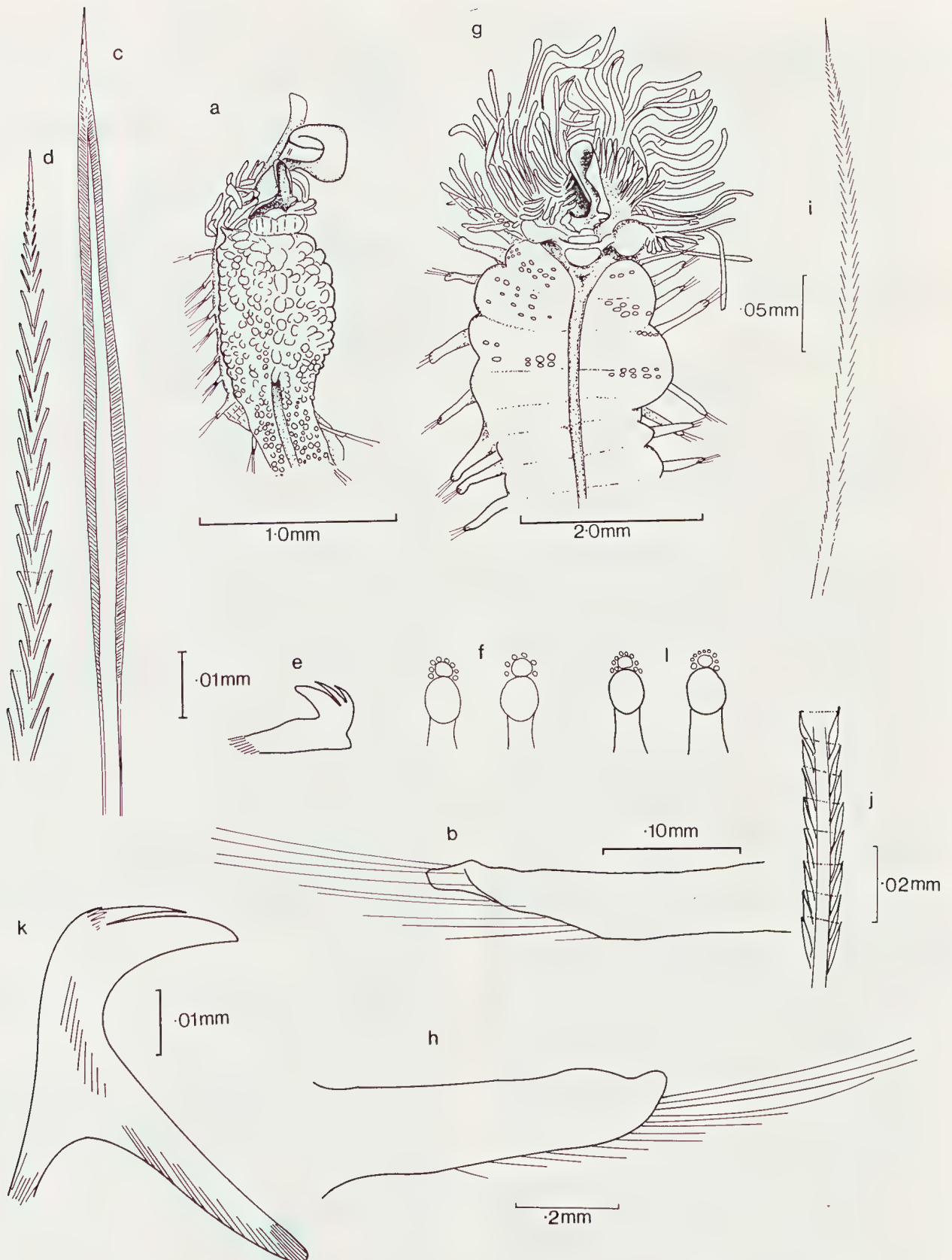


Fig. 6. *Polycirrus bicirinalis* n. sp., holotype: **a**, ventral view of head end; **b**, anterior view of notopodium 2, right side; **c, d**, two types of notosetae from same; **e**, lateral view of anterior uncinus; **f**, frontal views from same (schematic). *Polycirrus boholensis* (AM W199624): **g**, ventral view of head end; **h**, anterior view of notopodium 3, left side; **i, j**, notoseta from same; **k**, lateral view of midabdominal uncinus; **l**, frontal views from same (schematic).

of minute teeth surmounting this, and the ventrolateral region of the thorax with very few papillae. Grube stated that the species has 11–12 (possibly 13) pairs of notopodia, although we could only detect 10–11 pairs on his specimen. The structure of both the notosetae and uncini of the holotype closely resembles the Australian material. *Polycirrus bohollensis* can be separated from other Australian species using the characters shown in Table 1.

Habitat. Coral reef substrata, lagoon and reef slope, in 3–12 m.

Distribution. Queensland (Fig. 12F). Philippines. First record of species since the original description.

Polycirrus broomensis

Fig. 7a–c

Polycirrus broomensis Hartmann-Schröder, 1979: 148–149, fig. 352–354; 1980: 78.

Material examined. HOLOTYPE: (HZM P-15532), Western Australia, Broome; incomplete, about 35 mm long according to Hartmann-Schröder, with about 32 segments, 2.5 mm wide.

Description. Body large, coiled. Dorsum faintly annulated on first few segments. Ventrum glandular laterally on setigers 1–9, distinct ventrolateral pads absent, except for a single reduced pad present on setiger 10. Epidermis of lateral ventrum smooth, irregularly dissected. Midventral groove deep, wide on thorax, narrowing posteriorly, extends along entire body. Tentacular membrane trilobed, free from upper lip distally, with numerous tentacles of varying thickness.

Notopodia from segment 2–3; it is difficult to decide the numbering of segments on the holotype as segmentation is very poorly defined, probably because of the lack of anterior septa; 12 pairs of notopodia. Notopodia large, stout rectangular processes longest on midthorax, with notosetae arranged in a wide transverse series, in 2 tiers; long narrow winged capillaries appearing faintly hirsute under 40x (Fig. 7a) and shorter (about 1/2 length) pinnate setae (Fig. 7b); approximately equal numbers of each setal type. Uncini from first abdominal segment (segment 14–15) arranged on broad, rectangular pinnules, similar sized throughout. Each neuropodial row with many uncini, posterior ones with more than 100. Uncini with flat base and short thick neck and a characteristic upward projecting button below main fang (Fig. 7c); dental formula MF: 1:1, occasionally MF: 1:1–2.

Nephridial papillae minute at the ventral base of the notopodia present on setigers 3–8.

Comments. The original description of *P. broomensis* has been somewhat expanded to include additional comments on setae and ornamentation of the epidermis. Hartmann-Schröder was also unable to ascertain the segment of first appearance of the notopodia, stating that it could be segment 2 or 3. Surprisingly there has only been one additional record of the species (Hartmann-Schröder, 1980), despite the sampling of

similar habitats to the type locality along the Western Australian coast.

Habitat. Mangrove mud flats, associated with plant detritus.

Distribution. Broome, Western Australia (Fig. 12F).

Polycirrus disjunctus n. sp.

Figs 7d–l; 12D

Material examined. HOLOTYPE: New South Wales, Solitary Island, 29°56'S 153°25'E, (AM W199632); complete, 52 segments, 13.8 mm long, 1.6 mm wide. PARATYPES: New South Wales, Seal Rocks, 32°28'S 152°33'E, 1(AM W199633); South West Rocks, 32°25'S 152°32'E, 1(BMNH ZB 1985.27); Angourie Point, 29°29'S 153°22'E, 1(USNM 098822), 2(AM W199634). Paratypes range in width from 0.6–1.0 mm. BMNH ZB 1985.27 is ovigerous.

Description. Body gradually tapering from midthorax to end of body, a shallow midventral glandular streak throughout. Thoracic epidermis smooth dorsally, lightly papillated ventrally. Ventrolateral glandular pads extend from setigers 1–3 (Fig. 7d). Tentacular membrane trilobate with convoluted lateral lobes; free from upper lip distally. Peristomium difficult to discern dorsally and laterally, ventrally forms a small bluntly conical projecting lower lip (Fig. 7d).

Segment 2 achaetous, indistinct dorsally, 1/4–1/3 of the length of segment 3 ventrally. Notopodia from segment 3, 11 pairs; notopodia reduced in length posteriorly to about 2/3 length of anterior ones (Fig. 7e). Notoetae of segments 3–5 (setigers 1–3) long pinnate capillaries with smooth shafts, graded in length (Fig. 7f,g); notosetae of segments 6–13 (setigers 4–11) shorter, hirsute, graded in length (Fig. 7h,i). Neuropodia from segment 15 (setiger 13) continue to pygidium; neuropodial lobes elongate, rectangular lamellae, becoming slightly more elongate posteriorly. Uncini with broad concave base, long narrow neck (Fig. 7j), dental formula MF: 3–6 (Fig. 7k); initially 7–9 uncini per row, increasing up to 11–12 uncini per neuropodial row on midabdomen.

Nephridial papillae minute, arising from raised areas at the base of notopodia on setigers 5–9. Pygidial segment minute, anus terminal.

Variation. Paratypes with ventrolateral glandular pads on first 2–3 setigers. Segment 2 not visible in some specimens. Notopodia extending for 10–11 segments; notopodial lobes either smooth, rounded distally or with a small, rounded postsetal lobe. Notoetae are long pinnate capillaries on setigers 1–3, slightly shorter, hirsute capillaries on setigers 4–11 on all paratypes. Uncini from segment 10–14, show slightly greater variations in the number of teeth in the second row than the holotype, MF: 3–8. All uncini from paratype material with delicate tendons attached to the base and extending into the neuropodia (Fig. 71); these tendons not seen in the holotype.

Nephridial papillae elongate, minute, present on the

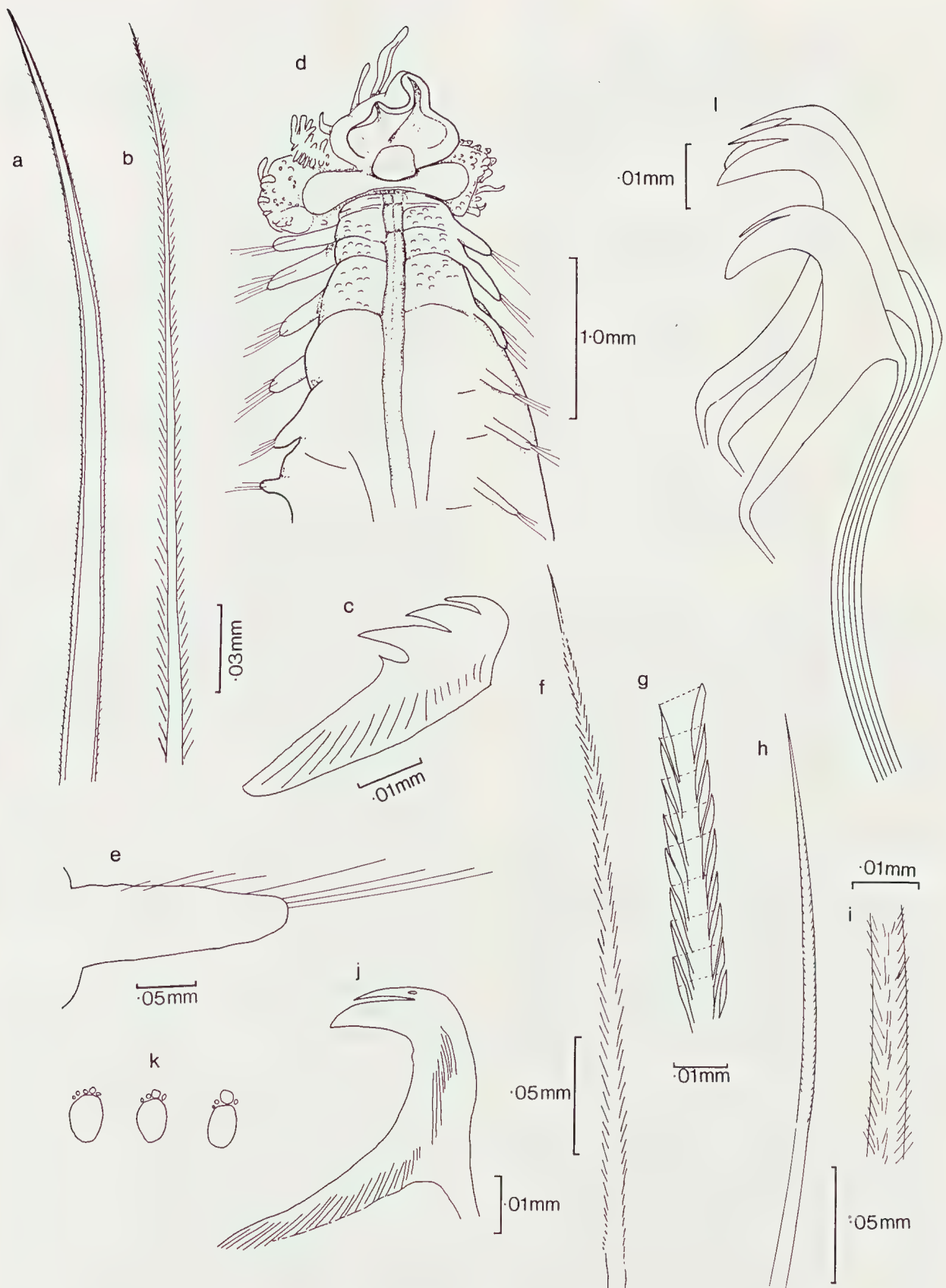


Fig. 7. *Polycirrus broomensis*, holotype: a, b, two types of notoseta; c, lateral view of midabdominal uncinus. *Polycirrus disjunctus* n. sp., holotype: d, ventral view of head end; e, anterior view of notopodium 3, right side, f, g, notoseta from same; h, i, notoseta from notopodium 10; j, lateral view of midabdominal uncinus; k, frontal views from same (schematic); l, lateral view of uncini showing tendons attached (striations omitted).

anteroventral base of notopodia 7–11 in an ovigerous specimen.

Comments. *Polycirrus disjunctus* can be distinguished from other Australian species of *Polycirrus* using the characters as shown in Table 1. It differs from *P. aquila* Caullery, 1944, described from the Malay Archipelago, and *P. nervosus* Marenzeller, 1884, from Japan, with regard to the numbers of pairs of notopodia and the type of notosetae present.

Habitat. Intertidal to 15 m, rocky substrata, associated with ascidians, or in one case, on algal mat exposed to surf.

Distribution. New South Wales (Fig. 12D).

Etymology. The specific name is derived from the latin *disjunctus* meaning separate, distinct, different, remote referring to the separate occurrence of the two types of setae, one from the anterior and one from subsequent notopodial fascicles.

Polycirrus nephrosus n. sp.

Figs 8a–f; 12E

Polycirrus boholensis.—Augener, 1914: 102–106, text fig. 14a–c. Not Grube.

Material examined. HOLOTYPE: New South Wales, Port Hacking, Ship Rock, 34°04'S 151°06'E, (AM W199641); complete, 37 segments, 27 mm long, width 1.2 mm. PARATYPES: Western Australia, Port Gregory, 28°12'S 114°15'E, 1(USNM 098823), King George Sound, Albany, 35°03'S 117°58'E, 1(BMNH ZB 1985.228); New South Wales, Towra Point, Botany Bay, 33°58'S 150°59'E, 2(AM W199642); Queensland, Stradbroke Island, Myora, 27°31'S 152°35'E, 1(QM G4056). Paratypes range in width from 1.3–2.7 mm.

Description. Body long, slender, gradually tapering posteriorly from posterior thorax. Segments relatively long, up to twice body width anteriorly. Dorsum anteriorly annulated with up to 12 rings per segment, faintly tessellated; ventrum with a deep midventral groove, extending from segment 2 posteriorly; lateroventrum smooth, inflated, pads absent (Fig. 8a), tentacular membrane large, trilobate, lateral lobes convoluted, extending back to first pair of notopodia. Upper lip free from tentacular membrane. Peristomium ventrally forming a protruding triangular lower lip (Fig. 8a).

Notopodia from segment 2–3, 18 pairs, last 2–3 with very few, short setae; notopodia elongate, distally knobbed and slightly recurved (Fig. 8b), decreasing in length from almost equal body width initially to ½ body width by setiger 7 to papilliform processes by setiger 14. Notosetae long, slender, coarsely hirsute capillaries (Fig. 8c,d). Neuropodia from setiger 12, present on all subsequent segments; neuropodial lobes initially papilliform, located at ventral base of notopodia, increasing in size slightly, posteriorly. Uncini with broad slightly concave base, moderate length, slender neck (Fig. 8e) and dental formula MF: 3–7, with medial tooth

(teeth) largest (Fig. 8f). Uncini arranged in single, very short rows (8–15 per row).

Nephridial papillae paired lateral processes on setigers 2–14 positioned as follows – setiger 2: anterior base of parapodia; setigers 3–9: anterior base of parapodia plus 1 pair of internotopodial papillae; setigers 10–14: 2 pairs of internotopodial papillae (Fig. 8a).

Pygidium with an encircling ring of small papillae situated around terminal anus.

Variation. Paratypes (USNM 098823, QM G4056) significantly larger than holotype. The following variation was shown in the paratypes: annulations extending on to ventrum, irregular papillation on ventrolateral inflated areas; lower lip tongue-like, distally rounded, recurved posteriorly; notopodia with elongate dorsally directed lobes, 14–26 pairs; uncini from segment 12–16, no greater variation in dental formula than for holotype. Arrangement of nephridial papillae variable, Port Gregory specimen as follows – setiger 2: anterior base of parapodia; setigers 3–12: anterior base of parapodia plus 1 pair of interparapodial; setigers 13–15: anterior and posterior base of parapodia and 1 pair of interparapodial. Myora specimen (QM G4056) as follows – setiger 2: anterior base of parapodia; setigers 3–7: anterior base of parapodia plus 1 pair of inter-parapodial; setigers 8–9: anterior base of parapodia plus 2 pairs of interparapodial; setiger 10: anterior, posterior base of parapodia; setigers 11–14: ventral base of parapodia plus 2 pairs of interparapodial papillae. Paratypes from Botany Bay (AM W199642) and King George Sound (BMNH ZB 1985.228) show a similar arrangement of nephridia with most thoracic segments having 2 pairs each of large nephridial papillae.

Comments. *Polycirrus nephrosus* has notopodia beginning on either segment 2 or 3. The precise numbering of segments in this region of *P. nephrosus* is difficult to interpret because of the lack of a clear demarcation of segments dorsally at least from the exterior. No attempt was made to examine the segmentation histologically.

The type material of *P. nephrosus* represents a considerable variation in size, and all the material regardless of size shows a similar development of nephridial papillae which are particularly conspicuous in this species. However it is not known whether very small individuals possess such well developed nephridial papillae. This species reaches a considerable size in comparison to other species of *Polycirrus* recorded from Australia, and in this species the number of pairs of notopodia does not tend to decrease with increasing body size, as in other Australian *Polycirrus* species.

Polycirrus nephrosus can be distinguished from other species of Australian *Polycirrus* using the characters given in Table 1. It can be distinguished from *P. aquila* Caullery, 1944, by the type of notosetae, which are coarsely hirsute in *P. nephrosus* and pinnate in *P. aquila*, and by the arrangement of nephridial papillae.

Habitat. In association with sponges, soft and hard

corals, empty mussel shells, algae; intertidal to 10 m.

Distribution. Western Australia, New South Wales and Queensland (Fig. 12E).

Etymology. The specific name refers to the large number of nephridial papillae present.

Polycirrus octoseta new combination

Figs 8g–l; 12D

Litancyra octoseta Hutchings, 1977: 10, fig. 4a–d.

Material examined. HOLOTYPE: Queensland, Moreton Bay, Serpentine Creek (AM W6852). PARATYPE: New South Wales, Belmont Beach (AM W8127). Western Australia, North West Shelf, off Port Hedland, 20°23'S 118°37'E, 1(AM W199545), 1(AM W199547), 2(AM W199546), 1(AM W199548); Bass Strait, 39°08'S 143°24'E, 77 m, 1(NMV F50351); 39°28'S 143°17'E, 103 m, 1(NMV F50352), 3(NMV F50353). Material ranged in size from 39 segments, 3.0 mm long, 0.5 mm wide to about 66 segments, 22 mm long, 0.9 mm wide.

Comments. Both the holotype and paratype were examined and compared with the present material. The North West Shelf material has nine pairs of notopodia, beginning on segment 3, whereas the Bass Strait material has eight pairs of notopodia, like the types. Notosetae in the present material consist of winged, spatulate capillaries and shorter, slender, tapered capillaries, appearing smooth under 40x (Fig. 8g) and hirsute under 100x objective (Fig. 8h,i). Uncini have four rows of teeth surmounting a small main fang (Fig. 8j), appearing identical to those of the types. The dental formula is difficult to discern as the teeth are very small and close together in each row (Fig. 8k). Bass Strait specimens showed the following variation in the dentition of the uncini MF: 1–3:1–3:2:1; maximum number of uncini per row 32–38.

Hutchings (1977) erected the genus *Litancyra* for a species with long handled uncini and lacking well defined midventral pads. It now appears, however, that the long, slender tendons attached to the base of each uncinus extending through the neuropodia are present in all *Polycirrus* examined herein (eg. Figs 7l,8l). The tendons are easily broken and much more slender than the long handled uncini found in some members of the Amphitritinae.

The degree of development of ventral glandular pads appears to be a variable character within the Polycirrinae. In the species of *Amaeana* and *Lysilla* examined, midventral pads are well developed, yet in the genus *Polycirrus* the ventrolateral areas are more glandular and pad-like, although the degree of development of these ventrolateral pads is variable. The lack of well defined midventral glandular pads in *Litancyra* is therefore not now considered a valid generic character, and *L. octoseta* is transferred to the genus *Polycirrus*, and the genus *Litancyra* is synonymised with *Polycirrus*.

Polycirrus octoseta may be distinguished from other

Polycirrus species in having a very long, medially expanded tentacular lobe, fused with the upper lip and without lateral lobes; notosetae of two types: slender, tapered capillaries and spatulate capillaries; and uncini with four rows of teeth surmounting the main fang, each row with a few teeth. In this latter respect it resembles *P. latidens* Eliason, 1962, from Skagerak, Denmark, which has teeth arranged in a vertical series above the main fang.

Habitat. Intertidal estuarine and exposed beaches of eastern Australia, and in 36–41 m off North West Shelf.

Distribution. Western Australia, Bass Strait, New South Wales and Queensland (Fig. 12D).

Polycirrus parvus n. sp.

Figs 9a–e; 12E

Material examined. HOLOTYPE: Western Australia, North West Shelf, off Port Hedland, 20°23'S 118°37'E, (AM W199628); incomplete, 27 segments, 5.1 mm long, 0.7 mm wide. PARATYPES: North West Shelf, off Port Hedland 2(AM W199631), 1(AM W199630), 1(AHF Poly 1456), 1(BMNH ZB 1985.229), 1(USNM 098824). Paratypes range in size from about 38 segments, 2.5 mm long, 0.3 mm wide to about 45 segments, 6.2 mm long, 0.7 mm wide.

Description. Body very small, tapering gradually posteriorly from about the midthoracic region, and slightly inflated on posterior abdomen. Epidermis of anterior dorsum faintly tessellated. Ventrolateral glandular pads on setigers 1–7 smooth, separated by a shallow midventral groove which extends along the entire body (Fig. 9a). Tentacular membrane weakly trilobate, lateral lobes reduced to a small tubercle, medial lobe fused with upper lip; posteriorly the tentacular membrane forming a slightly raised dorsal collar. Peristomium equal in length to segment 2 dorsally, ventrally it forms a pentagonal lower lip (Fig. 9a).

Segment 2 achaetous, reduced laterally to a small wedge-shaped pad, absent ventrally. Notopodia from segment 3, 10 pairs; notopodial lobes similar throughout, short with an elongate, digitiform postsetal lobe and a very small, pointed presetal lobe (Fig. 9b). Notosetae slender, winged capillaries, expanded slightly subdistally, distally minutely hirsute, setae arranged in graded lengths (Fig. 9c). Neuropodia from segment 14; extending posteriorly to at least segment 27; neuropodial lobes elongate, rectangular lamellae, increasing in length posteriorly to extend just beyond posterior edge of segment. Uncini with a flat base, short, thick neck and slight hump below the main fang (Fig. 9d); dental formula MF: 2–5:5–6, with the medial tooth in the first row largest (Fig. 9e). Uncini arranged in single, curved rows, initially about 20 per row increasing to about 30 per row on midabdomen; attachment tendons of uncini distinct, visible with x10 magnification, and extending to the base of neuropodial lobe.

Nephridial papillae absent.

Variation. Paratypes often with thorax inflated and

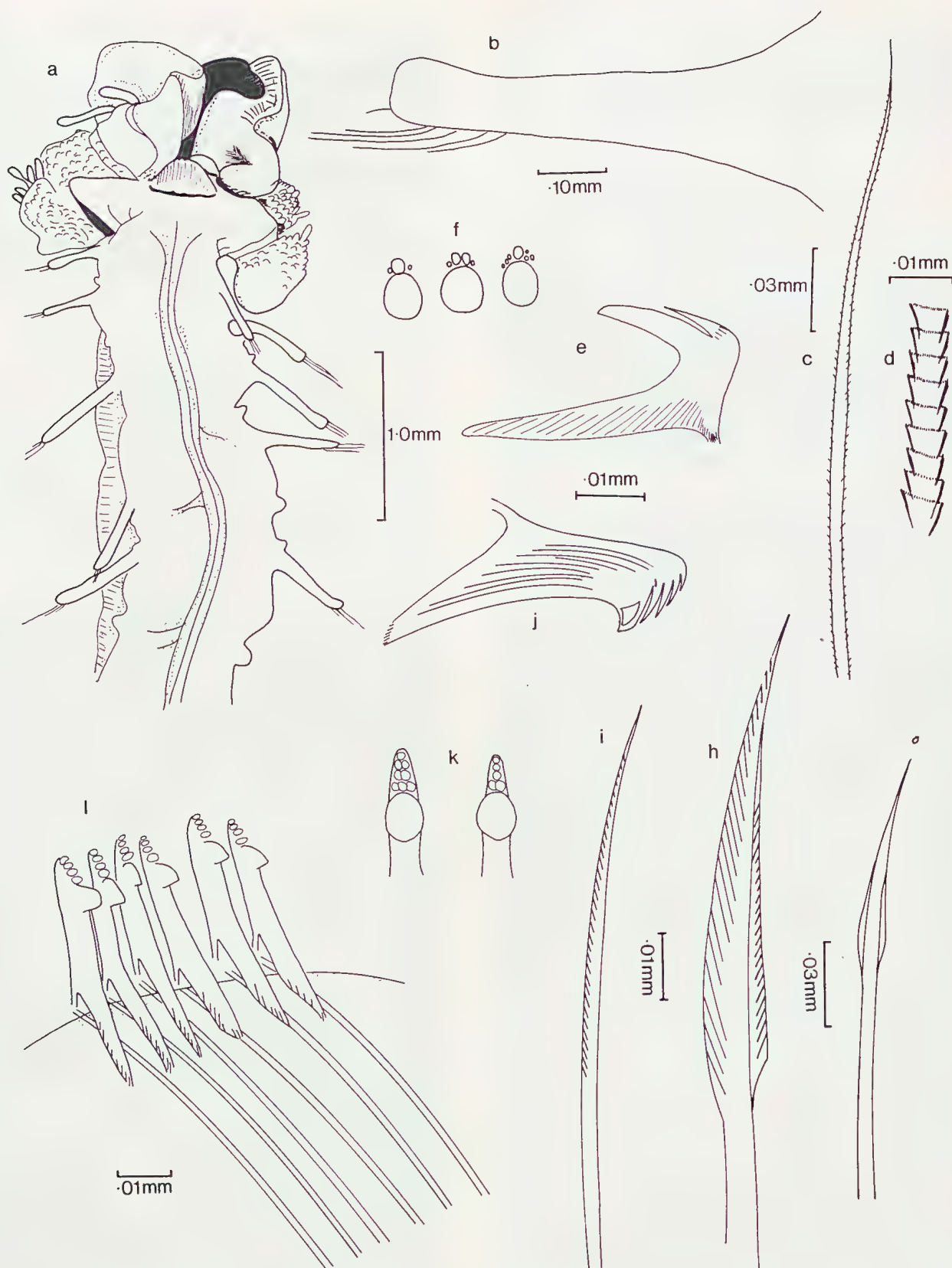


Fig. 8. *Polycirrus nephrosus* n. sp., holotype: a, ventral view of head end; b, posterior view of notopodium 3, left side; c, d, notoseta from notopodium 2; e, lateral view of midabdominal uncinus; f, frontal views from same (schematic). *Polycirrus octoseta* n. comb., paratype (AM W8127): g, h, winged type notoseta; i, wingless type notoseta; j, lateral view of uncinus from midabdomen; k, frontal views from same (schematic); l, frontolateral view of uncini in situ showing tendons (details of dental formula omitted).

abdomen uniformly tapered. Thoracic epidermal pattern indistinct on small animals; one paratype with some irregularly arranged small papillae on ventrolateral pads. Ventrolateral pads on first 5–7 setigers occasionally meet medially, depending on state of contraction of body. Notopodia extending from segment 9 to 13; shape of podia variable, occasionally with distal lobes retracted. Uncini commence on segments 12–18, extending to pygidium; maximum number of uncini per row 15–30; dental formula varies from MF: 2–5:3–6 to MF: 3–6:5–7. Nephridial papillae absent.

Comments. *Polycirrus parvus* can be distinguished from other Australian species of *Polycirrus* by the characters shown in Table 1. The species is characterised by its small size, relatively few pairs of notopodia and the single type of notoseta present.

Habitat. Sandy sediments in 40–80 m.

Distribution. Western Australia (off Port Hedland) (Fig. 12E).

Etymology. The specific name is derived from the latin *parvus* meaning 'little' referring to the small size of the species.

Polycirrus paucidens n. sp.

Figs 9f–l; 12D

Material examined. HOLOTYPE: Bass Strait (NMV F50348); complete, about 50 segments, 10.2 mm long, 1.2 mm wide. PARATYPES: Bass Strait 1(AM W199635), 1(AM W199636), 1(USNM 098825), 2(BMNH ZB 1985.218), 1(NMV F50358). Paratypes incomplete, range in width from 0.4–1.0 mm. All type material from Stn 202, 39°00'2S 144°33'9E, 60 m.

Description. Body short, thorax slightly inflated, abdomen gradually tapering; a deep segmented midventral glandular groove throughout. Thoracic epidermis heavily papillated dorsally and anteroventrally (Fig. 9f,g). Ventrolateral glandular pads poorly developed. Tentacular membrane trilobate, medial lobe largest, fused with upper lip; tentacular membrane dorsally transversely grooved, distal margins entire, becoming convoluted proximally; lateral lobes of tentacular membrane extremely reduced. Peristomium equal in length to segment 2 dorsally, absent laterally, forming an oval shaped lower lip ventrally (Fig. 9f).

Segment 2 achaetous, half the length of segment 3 laterally and ventrally. Notopodia from segment 3, small, with a minute digitiform postsetal lobe, 7 pairs (Fig. 9h). Notoetae smooth, slender, wingless capillaries (Fig. 9i). Neuropodia from segment 14; neuropodial lobes rectangular lamellae directed posteriorly from body wall, extending to posterior edge of segment. Uncini with a broad, slightly concave base and short, thick neck (Fig. 9j,k), dental formula MF: 1–3 (Fig. 9l); uncini arranged in single, straight rows on distal edge of neuropodial lobes; maximum number of uncini per row 8–22.

Pygidial segment minute, anus terminal.

◀ **Variation.** Paratypes with ventrolateral region of thorax glandular, but not forming distinct pads. Shape of medial lobe of tentacular membrane variable, often highly elongated. Notopodia extend for 7–9 segments; postsetal notopodial lobe may be retracted. Notoetae wingless capillaries, usually showing a slight subdistal expansion. Uncini begin on segment 13–17, continuing to near pygidium; dental formula shows no greater variation than for holotype. Nephridial papillae absent.

Comments. *Polycirrus paucidens* can be separated from the other Australian species of *Polycirrus* using the characters shown in Table 1. It most closely resembles *P. octoseta* (Hutchings, 1977) but can be distinguished from it by the type of notosetae present, and the papillated dorsum of *P. paucidens* in contrast to the smooth dorsum of *P. octoseta*.

Habitat. Continental Shelf at 27–171 m depth, from clayey sand to very coarse sand with shell fragments.

Distribution. Bass Strait (Fig. 12D).

Etymology. The specific name is derived from the latin *paucus*, meaning few or little, and *dens*, meaning tooth, referring to the small number of teeth surmounting the main fang of the uncinus.

Polycirrus porcata

Figs 10a–d; 12F

Polycirrus porcata Knox & Cameron, 1971: 36, figs 30–31. *Polycirrus* sp. 1 Mahon, 1973: 371.

Material examined. HOLOTYPE: (NMV G1757), Quiet Corner, Port Phillip Bay, Victoria. South Australia: Little Island 8(AM W199485); Kangaroo Island, Western River Cove 1(AM W199483). Tasmania: Maria Island 1(AM W199484). Bass Strait: 1(NMV F60338), many(NMV F50340), 1(NMV F50339). Victoria: Port Phillip Bay 1(AM W16128), 1(AM W16129), 1(AM W16130), 5(AM W16223), 1(NMV F50341), 8(NMV F50343); Western Port Bay, Crib Point 1(NMV F50344), 2(NMV F50342), 1(NMV F50347), Crawfish Rock 2(NMV F50346), 1(NMV F50345). Specimens ranged in size from about 25 segments, 2.0 mm long, 0.8 mm wide, to an ovigerous female about 71 segments, 34 mm long, 3.6 mm wide.

Comments. The type description given by Knox & Cameron (1971) differs somewhat from the holotype which was re-examined. Uncini first appear on segment 6 (setiger 4) not segment 10 (setiger 8) as stated by Knox & Cameron, and they occur at the ventral base of the notopodia. Thoracic uncini have a dental formula MF: 3–4 and appear to have, in profile, a single elongate tooth surmounting the main fang (Fig. 10a). Abdominal uncini are much larger than thoracic ones and show greater development of a tooth below the main fang. They appear to have a second row surmounting the main fang consisting of a series of minute teeth (Fig. 10b).

Thoracic notosetae appear finely hirsute under 40x, significantly so under 100x, and do not appear to be winged as suggested by Knox & Cameron (Fig. 10c,d). There are 12 pairs of notopodia beginning on segment 3. Nephridial papillae are prominent as elongated

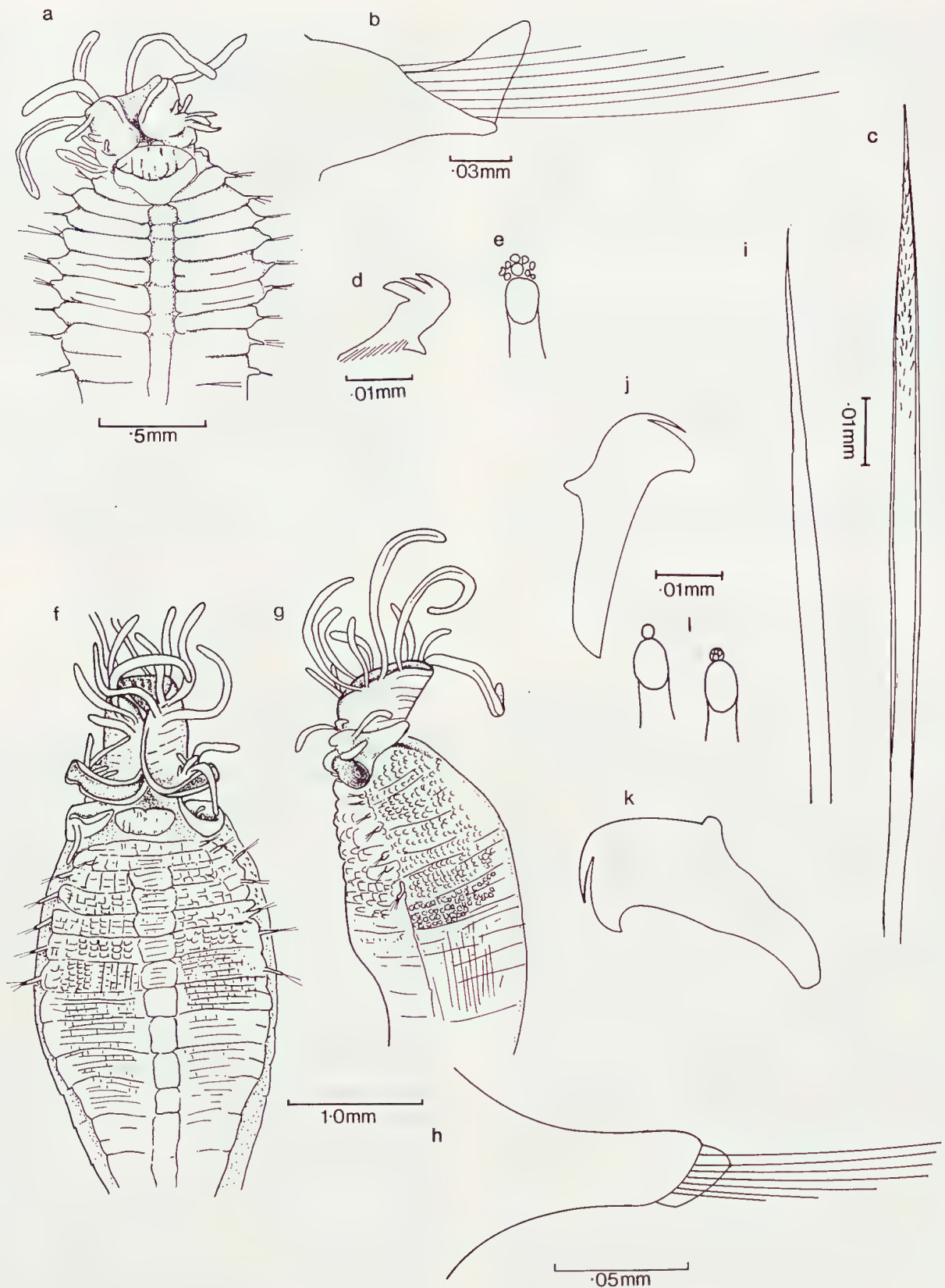


Fig. 9. *Polycirrus parvus* n. sp., holotype: a, ventral view of head end; b, anterior view of notopodium 4, right side; c, notoseta from same; d, lateral view of uncinus from midabdomen; e, frontal view from same (schematic). *Polycirrus paucidens* n. sp., holotype: f, ventral view of head end; g, lateral view of same; h, anterior view of notopodium 3, left side; i, notoseta from same; j, k, lateral views of uncini from anterior and midabdomen respectively; l, frontal views of uncini from midabdomen (schematic).

processes occurring on the anterior base of notopodia on setigers 2–12, i.e. 11 pairs of papillae are present, not 9 pairs as reported by Knox & Cameron (1971).

Other material examined was generally much smaller than the holotype and exhibited the following variations: ventrolateral glandular pads absent or slightly developed on first 4 setigers; epidermis irregularly and lightly papillated. Notopodia from segment 3, extending for 9–11 segments with the numbers appearing to increase with increasing body size. Uncini from segment 5–7, initially 3–5 uncini per neuropodium, increasing up to 8–10 uncini in abdominal segments. Uncini increase in size posteriorly; dental formula MF: 3–5 (thorax) (Fig. 10e), MF: 1:6–12 (abdomen) with the most distal teeth minute. Nephridial papillae prominent, absent in smallest specimens, beginning on setiger 1–4, extending to last notosetigerous segment.

Polycirrus porcata can be distinguished from other Australian species of *Polycirrus* using the characters shown in Table 1. The distribution and habitats from which the species has been recorded have been considerably expanded from the original type locality of Port Phillip Bay.

Habitat. Intertidal to about 100 m, sheltered bays and on the continental shelf; mainly from soft sediments ranging from silty clay-sand to sandy gravel and coarse shell. Associated with the seagrass *Posidonia* in some shallow water areas.

Distribution. South Australia, Victoria, Bass Strait and Tasmania (Fig. 12F).

Polycirrus rosea

Polycirrus rosea Hutchings & Murray, 1984: 91–92, fig. 25, 1–5.

Comments. No additional material was found during this survey of Australian Polycirrinae.

Habitat. Estuarine mud at a depth of 4 m in a salinity of 33.4‰.

Occurrence. Known only from Hawkesbury River, New South Wales.

Polycirrus tessellatus n. sp.

Figs 10f–l; 12E

Material examined. HOLOTYPE: Victoria, Western Port Bay, 38°26'S 145°08'E, (NMV F50337); incomplete, 18 segments, 8.0 mm long, 2.0 mm wide. PARATYPES: South Australia, Elliston Reef, 33°39'S 134°53'E, 5(AM W199468), 1(AM W199469), Stokes Bay, 35°37'S 137°12'E, 1(AM W199470); Bass Strait Stn 170, 38°52.6'S 148°25.2'E, 140 m, 1(USNM 098826), Stn 164, 40°40.7'S 148°36.9'E, 67 m, 1(BMNH ZB 1985.219), Stn 115, 40°40'S 145°15'E, 32 m, 2(NMV F50332, F50333), Stn 113, 40°24'S 145°32'E, 65 m, 2(NMV F50334, F50335); Victoria, Western Port Bay, Crib Point, Stn 31N, 38°20.94'S 145°13.62'E, 15 m, 1(NMV F50336), Stn 32N, 38°20.83'S 145°13.49'E, 13 m, 1(AHF Poly 1457). Complete specimens range from about 40 segments, 10.0 mm long, 0.5 mm wide to about 80 segments,

15.5 mm long, 1.8 mm wide. Remaining paratypes range in width from 0.5–2.6 mm.

Additional material examined. South Australia: Kangaroo Island, Western River Cove, 1(AM W199472). Bass Strait: 1(NMV F50422), 1(NMV F50423), 1(NMV F50324), 1(NMV F50325), 1(NMV F50327), 1(NMV F50328), 2(NMV F50326), 1(NMV F50329), 1(NMV F50330). Victoria: Gabo Island 1(AM W199473). New South Wales: Minnie Water 1(AM W199471), Angourie Point 1(AM W199474).

Description. Thorax robust, tapering slightly beyond setiger 10. Dorsum of segments 1–5 and anterior segment 6 deeply tessellated, thereafter weakly annulated (Fig. 10f). Ventrals with a shallow glandular groove and lateral glandular pads on setigers 1–10 irregularly, deeply grooved, tessellated on lateral and medial margins; pads on setigers 8–9 reduced, barely visible on setiger 10 (Fig. 10g). Tentacular membrane expanded, fused with upper lip, distally with a frilly margin. Peristomial segment an incomplete ring; equal in length to segment 2 dorsally; absent laterally; forming a large, longitudinally grooved, crescent shaped lower lip ventrally (Fig. 10g).

Segment 2 achaetous; reduced laterally and ventrally to a thin glandular pad; absent midventrally. Notopodia from segment 3, 10 pairs; large triangular pre- and postsetal lobes (Fig. 10h). Notoetae narrow winged capillaries, smooth, some distally irregularly hirsute along one side as if worn (Fig. 10i,j). Neuropodia from segment 15; first few neuropodial lobes minute, lamellate, directed posteriorly. Uncini with slightly convex base and short, thick neck (Fig. 10k); dental formula MF: 1:6–12 (Fig. 10l); uncini arranged in single, straight rows, maximum number of uncini per row 22–40.

Nephridial papillae absent.

Variation. Paratypes exhibited considerable variation as follows: ventrolateral glandular pads deeply dissected or smooth, extending to setigers 7–13, with the last few reduced in size; midventral groove in this region present or obscured by pads. Segment 2 partially or wholly obscured ventrally by lower lip. Notopodia extending for 10–16 pairs depending on size of animal (see initial discussion of the genus *Polycirrus*); notosetae, narrow winged capillaries, appearing smooth or minutely hirsute under 40x objective, distinctly hirsute under 100x objective; wings occasionally splayed from wear, appearing irregularly hirsute; uncini from segment 10–16, dental formula highly variable between and within animals as follows: MF: 1–5: 5–17:α, with teeth in most distal row minute.

Abdomen of paratypes often slightly inflated with a shallow midventral groove; middle and posterior segments short, crowded; neuropodial lobes rectangular lamellae, almost equal to segmental length on posterior abdomen, extending to pygidial segment. Pygidium minute, anus terminal. Nephridial papillae present on some specimens on setigers 1–6 at the posteroventral base of notopodia.

Comments. *Polycirrus tessellatus* exhibits considerable

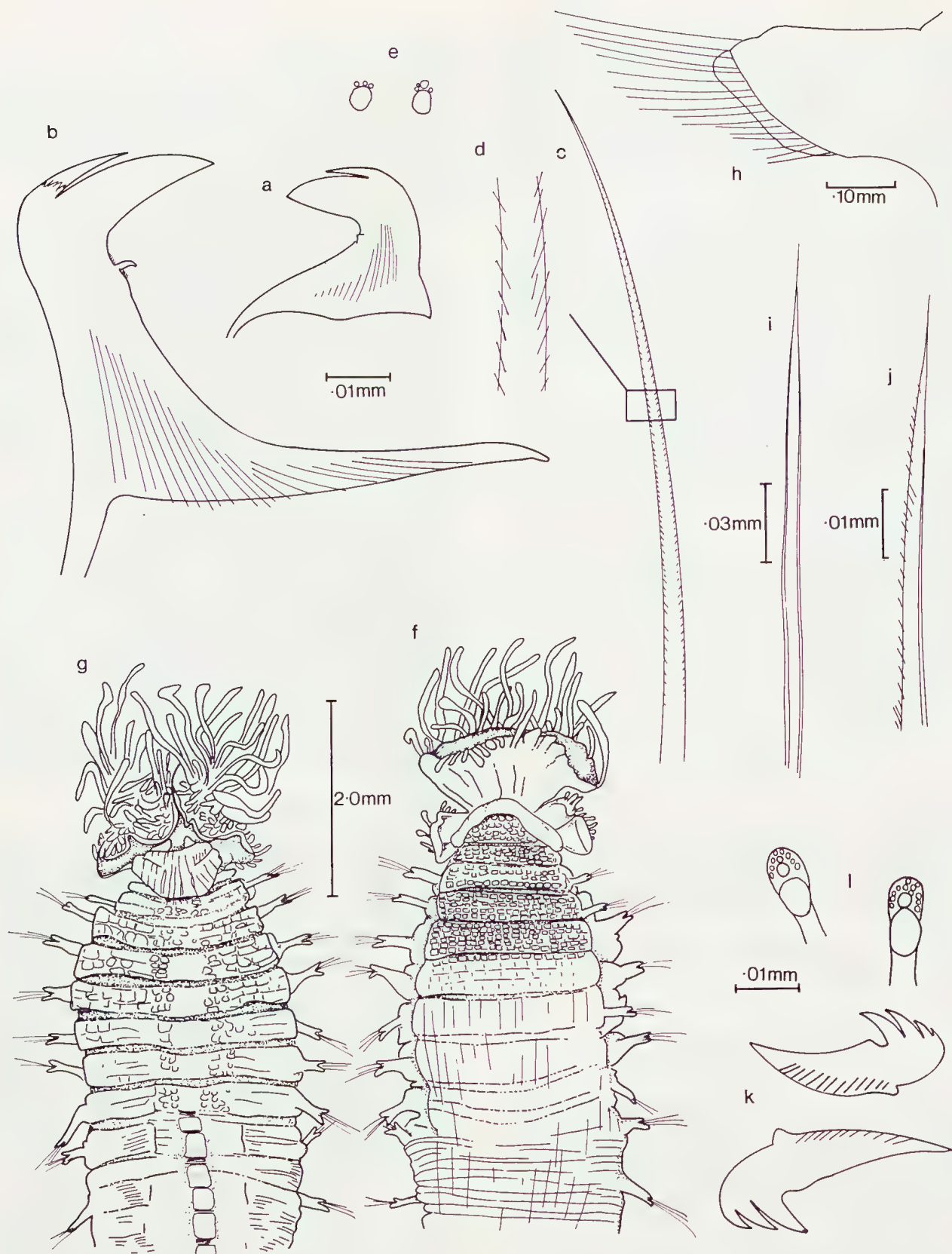


Fig. 10. *Polycirrus porcata*, holotype: a, lateral view of uncus from segment 7; b, lateral view of uncus from mid abdomen; c,d, notoseta from segment 7; e, frontal view of uncini from same. *Polycirrus tessellatus* n. sp., holotype: f, dorsal view of head end; g, ventral view of same; h, anterior view of notopodium 5, right side; i,j, notoseta from same; k, lateral views of uncini from midabdomen; l, frontal views of uncini from same (schematic).

variation within the material examined, in the numbers of pairs of notopodia present and the segment on which the uncini first appear. This is probably related to the size of the animal as explained in the initial discussion of the genus. It is therefore essential to look at a variety of other characters (Table 1) in order to distinguish this species from other Australian species of *Polycirrus*.

Habitat. Found on continental shelf in 27–130 m depth in sediment ranging from muddy sand to coarse sand. Also from exposed and sheltered rocky shores underneath rocks and associated with algal mats.

Distribution. South Australia, Victoria, Bass Strait and New South Wales (Fig. 12E).

Etymology. The specific name *tesselatus* is derived from the latin meaning inlaid with small square stones or mosaic, and refers to the epidermal pattern on the anterior dorsum.

***Polycirrus variabilis* n. sp.**

Figs 11a–g; 12E

Material examined. HOLOTYPE: Queensland, Lizard Island, 14°40'S 141°28'E, (AM W199538); complete, 57 segments, 10.6 mm long, 0.8 mm wide. PARATYPES: Lizard Island 1(USNM 098827), 1(AM W199540), 4(AM W199541), 2(AM W199539), 3(AM W199543), 1(AM W199544), 1(AHF Poly 1458), 1(AM W199477), 1(BMNH ZB 1985.230). Paratypes range in size from about 60 segments, 4.7 mm long, 0.4 mm wide to about 80 segments, 14.5 mm long, 0.8 mm wide.

Description. Body slender, filiform, gradually tapering posteriorly from midthorax. Dorsum faintly papillated anteriorly, ventrum glandular, deeply dissected on setigers 1–8. Ventrolateral pads absent. Midventral, glandular groove shallow, extending along entire body length (Fig. 11a). Tentacular membrane expanded medially, partially fused with upper lip, lateral

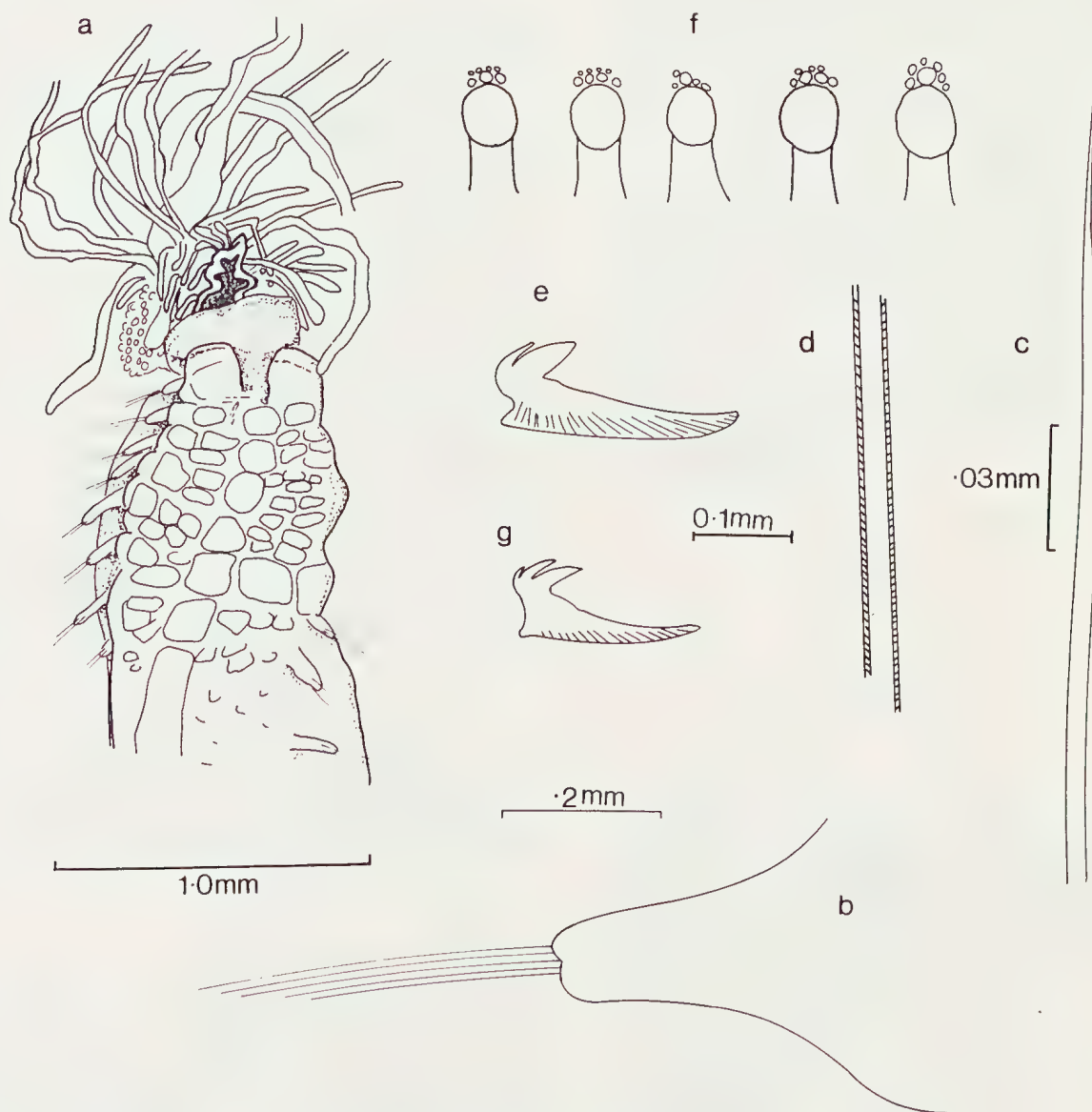


Fig. 11. *Polycirrus variabilis* n. sp., holotype: a, ventral view of head end; b, anterior view of notopodium 6, right side; c, d, notoseta from same; e, lateral view of uncinus from anterior abdomen; f, frontal views of uncini from same (schematic); g, lateral view of anterior abdominal uncinus from paratype (AM W199477).



Fig. 12. The Australian distribution of A, *Amaeana* species; B, *Hauchiella* species; C, *Lysilla* species; D-F, *Polycirrus* species.

lobes reduced. Peristomium very short dorsally, ventrally appearing bulbous, inflated; lower lip not distinct (Fig. 11a).

Segment 2 achaetous, reduced. Notopodia from segment 3, 15 pairs; notopodia short, slender, with minute rounded pre- and postsetal lobes (Fig. 11b). Notosetae slender, narrow winged capillaries, wings appear faintly striated under 100x objective (Fig. 11c,d). Neuropodia from segment 18 arranged in single, curved rows with 7–11 per row initially, increasing to about 22 on midabdomen; neuropodia rectangular lamellae initially, becoming longer and distally broader posteriorly. Uncini with a broad, flat to slightly convex base and short, thick neck (Fig. 11e); dental formula variable, as follows: MF: 1–5 :2–6, with medial tooth in first row often the largest (Fig. 11f).

Nephridial papillae absent. Pygidium with a minute ventral anal cirrus; anus terminal.

Variation. In smaller paratypes dorsal papillation not apparent. First 6–10 setigers ventrally glandular, in some cases the large glandular papillations resemble a body wall distended with eggs. Notopodia extending for 10–17 segments; some notosetae with faintly hirsute wings under 40x objective appear distally worn. Notopodia often with a small rounded presetal and slightly larger postsetal lobe. Uncini from segment 15–19, initially 6–8 per row, increasing up to 12–22 per row. Uncini sometimes with a minute second row visible in profile (Fig. 11g). Nephridial papillae absent.

Comments. *Polycirrus variabilis* can be separated from other Australian species of *Polycirrus* using the characters shown in Table I. The species most closely resembles *P. nervosus* Marenzeller, 1884, from Japan, especially in the form of the notosetae and uncini. The syntypes of this species (NMW Inv. no.1794) were examined and compared with *P. variabilis*. The two species differ most notably in the form of the ventrolateral glandular region, which is smooth and divided into distinct pads in *P. nervosus*, whereas in *P. variabilis* these pads are absent. Also, one syntype has 37–40 pairs of notopodia, significantly more than the number present in *P. variabilis*.

Habitat. Coral substrata in 7–12 m.

Distribution. Queensland, Lizard Island (Fig. 12E).

Etymology. The specific name *variabilis* is derived from the latin meaning changeable, referring to the large variation occurring in the dental formula of the uncini.

Discussion

The subfamily Polycirrinae is well represented in Australian waters, with 21 species in four genera. As mentioned in the introduction it seems likely that additional species occur in Australian waters. Exemplifying this potentially undescribed fauna, limited collections from the Bass Strait and North West Shelf, areas not well collected previously, have yielded two and three species respectively.

The genera *Lysilla*, *Amaeana* and *Hauchiella* contain relatively few species, and of these at least half of the known species in the world occur in Australia. The genus *Polycirrus* is well represented in Australian waters. At this stage it is difficult to ascertain what percentage of the *Polycirrus* fauna occurs in Australia because many of the currently described species may need to be synonymised. In some cases species may be *nomina nuda* unless additional material is collected, as some of the early descriptions are totally inadequate (Hutchings & Glasby, in prep). Other workers have also suggested the genus is in need of revision (Hartman, 1969; Banse, 1980). *Polycirrus* may also contain undescribed species as we suspect that some records have been confused in the literature.

Earlier workers divided *Polycirrus* into a number of subgenera. Caullery (1944) discussed in detail the three subgenera erected by Malmgren (1865), *Ereutho*, *Leucariste* and *Polycirrus*, and concluded that these subdivisions, based on the type and number of pairs of notopodia and the segment on which the uncini began, were valid. Our data clearly show (Table 1) that within a species there is sometimes a considerable range of segments over which the uncini begin and in the number of pairs of notopodia. This is partially related to the size of the animal and hence presumably age of the individual. Thus the subgenera as accepted by Caullery are not considered to be very useful. It seems likely that the segment on which the notopodia begin is a phylogenetic character, and should be used to split the genus into two. This should be confirmed by examining juvenile stages and will necessitate the detailed examination of the anterior segments of all species of *Polycirrus*. This is currently being undertaken (Hutchings & Glasby, in prep).

ACKNOWLEDGEMENTS. We would like to thank the following people for lending us material: D. George (BMNH), A. Muir (BMNH), K. Fauchald, (USNM), G. Hartmann-Schröder (HZM), R. Wilson (NMV), S. Rainer (CSIRO), L. Marsh (WAM), P. Mather (QM), S. Williams (AHF), E. Kritscher (NMW), L. Wallin (UZM), S. van der Spoel (ZMA), G. Hartwich (ZMB), L. Collett (NSWSF), I. Winsnes (ZMO); and L. Albertson and S. Perry for preparing the figures.

The Australian Bureau of Flora and Fauna provided the salary for one of us (CJG). We would also like to thank Queensland Electricity Generating Board for material and for permission to use their SEM photographs of *Lysilla bilobata*.

Table 1. Character states in *Polycirrus* species found, or expected to be found, in Australia. 1. General types of *Polycirrus* notosetae: A, Pinnate (e.g. Figs 6i,j); B, Hirsute (e.g. Figs 10c,d); C, Smooth, with narrow wings or wingless (e.g. Figs 8g,h; 9i; 11c,d). 2. General types of *Polycirrus* uncini: A, Concave base; long narrow neck; long main fang (e.g. Fig. 7j); B, Flat or slightly curved base; short, thick neck; short main fang (e.g. Fig. 10k).

Species	No. animals examined (max. width mm)	Ventrolateral glandular pads (No. pairs)	Notosetae		Uncini			Nephridial papillae (occurrence on setigers)		
			Appearance (seg.)	No. pairs	Type 1	Appearance (seg.)	Max. No. per row		Dental formula	Type 2
<i>P. aquila</i>	1(2.5)	poorly (6) developed	3	16	A	16	10	MF:3	A	present (2-16)
<i>P. bicrinalis</i>	8(0.9)	absent	3	14-16	A, C	17-20	15-25	MF:1:5-9	B	absent
<i>P. boholensis</i>	14(2.2)	indistinct	3	10-11	A	13-15	7-10	MF:1:3-12	A	present (1-11 or 2-11)
<i>P. broomensis</i>	1(2.5)	indistinct	2 or 3	12	A, B	14-15	>100	MF:1:1-2	B	present (3-8)
<i>P. disjunctus</i>	6(1.6)	present (2-3)	3	10-11	A, B	10-14	11-12	MF:3-8	A	present (7-11)
<i>P. nephrosus</i>	6(2.7)	absent	2 or 3	14-26	B	12-16	8-15	MF:3-7	A	present (2-15) most setigers with 2 pairs each
<i>P. octoseta</i>	12(0.9)	present (7)	3	8-9	C	11-12	32-38	MF:1-3:1-3:2-1	B	absent
<i>P. parvus</i>	7(0.7)	present (5-7)	3	9-13	C	12-18	15-30	MF:2-5:3-6	B	absent
<i>P. paucidens</i>	6(1.2)	indistinct	3	7-9	C	13-17	8-22	MF:1-3	B	absent
<i>P. porcata</i>	38(3.6)	poorly developed (4)	3	9-12	B	5-7	8-10	MF:3-5 (thorax) MF:1:6-12 (abdomen)	A	present (2-12)
<i>P. rosea</i>	1(0.5)	poorly (6) developed	3	10	C	10	8-10	MF:5-7:5-8	B	absent
<i>P. tessellatus</i>	15(2.6)	present (7-13)	3	10-16	C	10-16	22-40	MF:1-5:5-17	B	present (1-6)
<i>P. variabilis</i>	18(0.8)	poorly developed (6-10)	3	10-17	C	15-19	12-22	MF:1-5:2-6	B	absent

References

- Augener, H., 1914. Polychaeta II, Sedentaria. In 'Die Fauna Südwest Australiens Ergebnisse des Hamburger Südwest-australischen Forschungsreise' (W. Michaelsen & R. Hartmeyer, eds) 5(1): 1-700.
- 1918. Polychaeta Beiträge zur Kenntnis des Meeresfauna West-Afrikas. Herausgegeben von W. Michaelsen Hamburg 2: 67-625.
- 1926. Papers from Dr. T. H. Mortensen's Pacific Expedition 1914-1916. No. 34. Polychaeta III. Polychaeten von Neuseeland. II. Sedentaria. Videnskabelige Meddelelser fra Dansk naturhistorisk Føreling i Kjøbenhavn 81: 157-294.
- Banse, K., 1980. Terebellidae (Polychaeta) from the Northeast Pacific Ocean. Canadian Journal of Fisheries and Aquatic Sciences 37(1): 20-40.
- Benham, W.B., 1921. Polychaeta. Scientific Reports. Australian Antarctic Expedition 1911-14 (c) 6 (3): 1-128.
- Caullery, M., 1915. Sur les Terebelliens de la sous-famille Polycirridae Malmgr. 1. Delimitation des genres. 2. *Polycirrus arenivorus* n. sp. Bulletin de la Société Zoologique de France 40: 239-248.
- 1944. Polychètes sédentaires de l'Expedition du Siboga: Ariciidae, Spionidae, Chaetopteridae, Chloraemidae, Opheliidae, Oweniidae, Sabellariidae, Sternaspidae, Amphictenidae, Ampharetidae, Terebellidae. Siboga Expedition Leiden 24 (2): 1-204.
- Claparède, E., 1864. Glanures zootomiques parmi les Annélides de Port-Vendres (Pyrenées Orientales). Mémoires de la Société de physique et d'histoire naturelle de Genève 17(2): 463-600.
- 1870. Les Annélides Chetopodes du Golfe de Naples. Troisième partie. Société de physique et d'histoire naturelle de Genève. Mémoires 20(2): 365-542.
- Day, J.H., 1957. The polychaet fauna of South Africa. Part 4. New species and records from Natal and Moçambique. Annals of the Natal Museum 14(1): 59-129.
- 1961. The polychaet fauna of South Africa. Part 6. Sedentary species dredged off Cape Coasts with a few new records from the shore. Journal of the Linnean Society of London 44: 463-560.
- 1967. A monograph on the Polychaeta of Southern Africa. British Museum of Natural History Publications 656: 459-878.
- 1973. New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. NOAA Technical Reports NMFS Circular 375: 1-140.
- Day, J.H. & P.A. Hutchings, 1979. An annotated check-list of Australian and New Zealand Polychaeta, Archiannelida and Myzostomida. Records of the Australian Museum 32(3): 80-161.
- Ehlers, E., 1913. Die Polychaeten-Sammlungen der deutschen Südpolar Expedition 1901-1903. Deutsche Südpolar Expedition 13(4): 397-598.
- Eliason, A., 1962. Die Polychaeten der Skagerak-Expedition 1933. Zoologisk Bidrag från Uppsala 33: 207-293.
- Fauchald, K., 1977. The polychaete worms, definitions and keys to the orders, families and genera. Natural History Museum of Los Angeles County, Science Series 28: 1-190.
- Fauvel, P., 1927. Polychètes Sedentaires. Addenda aux Errantes Archiannelides, Myzostomaires. Faune de France 16: 1-494.
- 1928. Annélides polychètes nouvelle de l'Inde. Part 2. Bulletin du Muséum d'histoire naturelle 34: 159-165.
- Gravier, C., 1905. Sur deux types nouveaux de Terebelliens *Anisocirrus* nov. gen., *decipiens*, *Aponobranchus* nov. gen., *perrier* nov. sp. Bulletin du Muséum d'histoire naturelle 11: 437-444.
- 1907. Sur les Annélides polychètes recueillies par l'Expédition Antarctique française (Terebelliens, Serpuliens). Bulletin du Muséum d'histoire naturelle 13: 46-52.
- Grube, A.E., 1860. Beschreibung neuer oder wenig bekannter Anneliden Zahlreiche Gattungen. Archiv für Naturgeschichte 26: 71-118.
- 1878. Annulata Semperiana. Beiträge zur Kenntnis der Anneliden fauna der Philippinen nach den von Herrn Prof. Semper mitbrachten Sammlungen. Mémoires de l'Académie impériale des Sciences de St. Petersburg 25: IX + 300 pp.
- Hartman, O., 1944. Polychaetous Annelids from California including the descriptions of two new genera and nine new species. Allan Hancock Pacific Expedition 10: 1-290.
- 1959, 1965. Catalogue of the Polychaetous annelids of the world. Allan Hancock Foundation Occasional Paper 23: 628 pp. Supplement and index (1965) 197 pp.
- 1966. Polychaeta Myzostomidae and Sedentaria of Antarctica. Contribution No. 288 of the Allan Hancock Foundation. American Geophysical Union. Publication No. 1414, 158 pp.
- 1969. Atlas of the sedentary polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, 812 pp.
- Hartmann-Schröder, G., 1979. In G. Hartmann-Schröder & G. Hartmann, 1979. Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil 2. Die Polychaeten der tropischen Nordwest Küste (zwischen Derby im Norden und Pt. Hedland im Süden). Mitteilungen aus dem Zoologischen Museum in Hamburg 76: 77-218.
- 1980. In G. Hartmann-Schröder & G. Hartmann, 1979. Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil 4. Die Polychaeten der tropischen Nordwest Küste Australiens (zwischen Port Samson im Norden und Exmouth im Süden). Mitteilungen aus dem Zoologischen Museum in Hamburg 77: 41-110.
- Hessle, C., 1917. Zur Kenntnis der terebellomorphen Polychaeten. Zoologiska Bidrag från Uppsala 5: 39-258.
- Hutchings, P.A., 1974. Polychaeta of Wallis Lake, New South Wales. Proceedings of the Linnean Society of New South Wales 98(4): 175-195.
- 1977. Terebelliform Polychaeta of the families Ampharetidae, Terebellidae and Trichobranchidae from Australia, chiefly from Moreton Bay, Queensland. Records of the Australian Museum 31: 1-38.
- Hutchings, P.A. & C.J. Glasby, 1986. The genus *Euthelepus* (Terebellidae: Thelepininae) together with a description of a new species. Records of the Australian Museum 38(2): 105-117.
- in press. The Thelepininae (F. Terebellidae) from Australia together with a discussion of the generic and specific characters of the subfamily. Proceedings of The Biological Society of Washington.
- Hutchings, P.A. & A. Murray, 1984. Taxonomy of Polychaetes from the Hawkesbury River and the southern estuaries of New South Wales, Australia. Records of the Australian Museum Supplement 3: 1-118.

- Hutchings, P.A. & S.F. Rainer, 1979. The polychaete fauna of Careel Bay, Pittwater, New South Wales, Australia. *Journal of Natural History* 13: 745-796.
- Imajima, M. & O. Hartman, 1964. The Polychaetous annelids of Japan. Allan Hancock Foundation Occasional Paper 26: 1-452.
- Kinberg, J.G.H., 1866. *Annulata nova*. K. Svenska Vetenskapsakademien, Stockholm. *Ofversigt af Förhandlingar* 22: 167-179, 239-258.
- Knox, G.A. & D.B. Cameron, 1971. Port Phillip survey 1957-1963, Victoria, Australia. Part 2, No. 4. Polychaeta. *Memoirs of the National Museum, Victoria* 32: 21-42.
- Leidy, J., 1855. Contributions towards a knowledge of the marine invertebrates of the coast of Rhode Island and New Jersey. *Journal of the Academy of Natural Sciences, Philadelphia* 3: 135-158.
- Levensen, G.M.R., 1893. *Annulata, Hydroidae, Anthozoa, Porifera*. Vidensk. Udbytte af Kanonbaaden *Hauchs* Togter. Vidensk. København pp. 321-461.
- McIntosh, W.C., 1869. On the structure of the British Nemerteans, and some new British annelids. *Transactions of the Royal Society of Edinburgh* 25: 305-433.
- 1922. Notes from the Gatty Marine Laboratory St. Andrews, No. 44. 1. On new and rare Polychaeta from various regions. 2. Recent additions to the British marine Polychaeta. *Annals, Magazine Natural History London* (9) 9: 1-30.
- Mahon, B.P.G. (ed.), 1973. Environmental study of Port Phillip Bay. Report on phase I, 1968-1971. Sponsored by Melbourne and Metropolitan Board of Works, and Fisheries and Wildlife Department of Victoria, Melbourne, 372 pp.
- Malmgren, A.J., 1865. *Nordiska Hafs-Annulater Oefv. Forhandlingar Videnskabs Selskabet i Kristiania* 22: 344-410.
- Marenzeller, E. von, 1884. *Süd-japanische Anneliden* 11. *Denkschriften der Akademie der Wissenschaften, Wien* 49: 197-224.
- Milne Edwards, H., 1844. Observations sur le développement des Annélides faites sur les côtes de la Sicile. *Academie des Sciences, Paris, Compte rendus hebdomadaires des séances* 19: 1409-1426.
- Monro, C.C.A., 1930. Polychaete worms. *Discovery Reports* 2: 1-222.
- Okuda, S., 1940. Polychaetous annelids of the Ryukyu Islands. *Biogeographical Society of Japan, Bulletin* 10(1): 1-24.
- Quatrefages, A. de., 1865. Note sur la classification des annélides. *Academie des Sciences, Paris. Compte rendu hebdomadaire des séances* 60: 586-600.
- Rullier, F., 1965. Contribution à la faune des Annélides Polychètes de l'Australie. *Papers Department Zoology, University of Queensland* 2(9): 163-210.
- Saint-Joseph, A. de., 1894. Les Annélides polychètes des Côtes de Dinard. *Annales des sciences naturelles, Part 3 séries* 7, 17: 1-395.
- Sars, M., 1863. Geologiske og zoologiske lagttagelser, anstillede paa en Reise i en Deel af Trondhjems stift i Sommeren 1862. *Nyt magazin for naturvidenskaberne* 12: 253-340.
- Thorson, G., 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the sound (Øresund). *Meddelelser fra kommissionen for Danmarks Fiskeri-og. Havundersøgelser, Serie : Plankton, Bind 4 Nr. 1*. 1-523.
- Webster, H.E., 1879. Annelida Chaetopoda of the Virginian coast. *Transactions of the Albany Institute of New York* 9: 202-269.
- Wolfebaek, A., 1912. *Nordeuropaeiske Annulata Polychaeta*. 1. Ammocharidae, Amphictenidae, Ampharetidae, Terebellidae og Serpulidae. *Videnskabelige Akademie Kristiania, Skrifter Mathematisk Naturvidenskabelig Klasse* 1911(2): 1-144.

Accepted 16th June 1986

Some Majid Spider Crabs from the Deep Indo-West Pacific

D.J.G. GRIFFIN AND H.A. TRANTER

Australian Museum,
P.O. Box A285, Sydney South, NSW 2000, Australia

ABSTRACT. Fifteen species of seven genera are discussed. The material comes from depths exceeding 200 m in the Indian Ocean (off east Africa, Indonesia and north-west Australia) and the west Pacific (Tasman Sea and Kermadec Deep). Four new species are described, one of the genus *Platymaia* and three of *Rochinia*. The known geographic range of six species is extended: *Cyrtomaia suhmi*, *Pleistacantha moseleyi*, *Rochinia pulchra* are recorded from off north-west Australia for the first time. *Platymaia fimbriata* is recorded from the Indian Ocean for the first time and the known range of *Teratomaia richardsoni* is extended to the Kermadec region. *Echinoplax pungens* is confirmed as a synonym of *Pleistacantha moseleyi* and *Rochinia riversandersoni* is shown to be a complex of several species.

GRIFFIN, D.J.G. & H.A. TRANTER, 1986. Some majid spider crabs from the deep Indo-West Pacific. Records of the Australian Museum 38(6): 351-371.

The spider crab fauna of the Indo-West Pacific has been studied intensively by a number of people in the last 15 years (Griffin, 1976; Griffin & Tranter, 1974, 1986; Guinot & Richer de Forges, 1982a, 1982b; Kensley, 1977a, 1977b; Sakai, 1976; Serène & Lohavanijaya, 1973; Takeda, 1977, 1978, 1980; Yaldwyn & Dawson, 1976).

Deep water species are, as one would expect, less well known. We are pleased to have the opportunity therefore to study a number of collections.

The now famous *Galathea* Deep Sea Expedition left Copenhagen on October 15, 1950, and returned June 29, 1952. Its numerous and significant collections have been the subject of many reports. The deep-water spider crabs of the family Majidae have not been reported on previously. Dr Torben Wolff of the University Zoological Museum, Copenhagen kindly agreed to make the small but important collection from depths of 200 m or more available to us.

Australia's north-west shelf has assumed increasing importance in the last 10 years as a site of mineral exploration as well as a potentially important area for expansion of Australia's fishing industry. The *Soela*, chartered by CSIRO's Division of Fisheries, conducted investigations there from 1979 to 1983.

The Tasman Sea and areas around New Zealand have been explored over a number of years by the New Zealand Oceanographic Institute. The research vessel *Kapala* has engaged in exploratory fishing off NSW since 1971.

Material dealt with in this report is lodged in the Australian Museum, Sydney (AM), the Museum of Victoria, Melbourne (NMV), the Zoological Museum, Amsterdam (ZMA) and the University Zoological Museum, Copenhagen (ZMC). The dimension given for each specimen is carapace length (cl.) measured from the anterior tip of the rostrum, unless otherwise stated.

Subfamily INACHINAE

Achaeopsis Stimpson

Type species. *Achaeopsis spinulosus* Stimpson, 1857, by monotypy.

Remarks. Species of this genus are distinguished by the slender, simple postorbital spine. Only one species can be confirmed as occurring in the Australian and New Zealand area at present: previous records of

A. thomsoni from Australia therefore refer to *A. ramusculus*.

Distribution. West and east Atlantic, Indo-West Pacific.

Achaeopsis ramusculus (Baker)

Stenorhynchus ramusculus Baker, 1906: 104–106, pl. 1 figs 1, 1a.

Achaeopsis thomsoni.—Rathbun, 1918: 4, [Not *Dorhynchus thomsoni* Thomson, 1873 (see opinion 712: ICZN 1964).]

Achaeopsis ramusculus.—Hale, 1927: 124, fig. 121; Griffin, 1966: 35–37, fig. 4; Griffin & Tranter 1986: 21.

Material examined. One specimen, female, 14.7 mm, AM P35486, Tasman Sea, north-east of Wollongong, 34°24'S, 151°25'E, 738 m, demersal prawn trawl, FRV Kapala, stn K 76-23-01, 13 December 1976.

Remarks. The one complete rostral spine on this adult female clearly extends beyond the end of the peduncle of the second antenna, distinguishing it from *A. spinulosus* Stimpson and *A. rostrata* Sakai with shorter rostral spines. The protogastric and anteromedial branchial regions lack the spines present in *A. thomsoni* (Thomson). There is a very small tubercle on the protogastric region, and the anteromedial angle of the branchial region is smooth.

In this specimen the rostral spine is directed straight forward and slightly upwards. There are three small ventral spines on the rostrum – two in the proximal half and one in the distal half – as in the immature female specimen from New Zealand figured previously (Griffin, 1966: fig. 6.4). There is a small spine on the margin of the orbit, anterior to the preorbital spine, not present in other specimens of *A. ramusculus* we have examined. The ambulatory legs are missing from this specimen.

Miers (1886) identified a specimen collected by the *Challenger* from off Sydney (34°13'S, 151°38'E, 738 m, stn 164B) as conspecific with specimens of "*Lispognathus thomsoni* (Norman)" collected by the *Challenger* off South Africa. However, Miers expressed some reservation with this identification as the specimen was damaged and had 'one, not two spines on each branchial region'. It was noted previously (Griffin & Tranter, 1985) that this *Challenger* specimen could be either *A. ramusculus* or *A. rostrata*. At that time though, neither of these species had been recorded from the eastern coast of Australia. It seems not unreasonable to us that since *Kapala* obtained this specimen of *A. ramusculus* from almost exactly the same locality and depth as the specimen examined by Miers, the *Challenger* specimen was in fact *A. ramusculus*.

This is the first adult female reported for this species.

The status of the genus *Dorhynchus* was discussed by Manning & Holthuis (1981: 280–281); we regard it as synonymous with *Achaeopsis*.

Distribution. Southern and south-east Australia, and New Zealand.

Cyrtomaia Miers

Type species. *Cyrtomaia murrayi* Miers, 1886, by designation of Guinot & Richer de Forges, 1982b.

Remarks. One of the most characteristic, mainly West Pacific majid genera, *Cyrtomaia* contains 17 species, many requiring further study to clarify their status.

Distribution. Indo-West Pacific.

Cyrtomaia suhmi Miers

Figs 1–2

Cyrtomaia suhmi Miers, 1886: 16–17, pl. 3 fig. 2.—Griffin, 1974: 9–10; Griffin & Brown, 1976: 252–253, fig. 6; Guinot & Richer de Forges, 1982b: 21–24, figs 10, 11A–B, 23B; Griffin & Tranter 1986: 30–31, fig. 9e–g.

Material examined. One specimen, immature female, postrostral cl. 26.6 mm, ZMC, Danish *Galathea* Deep Sea Expedition, stn 324, Straits of Malacca, 6°06'N, 96°00'E, 1130 m, sledge trawl (ST 300), globigerina ooze, 9 May 1951; one specimen, ovigerous female, postrostral cl. 70 mm, AM P35487, Indian Ocean, north-west shelf of Australia, 250 km north-west of Port Hedland, 18°40'S, 116°42'E, 584–592 m, Engel trawl, J.R. Paxton on *Soela*, stn S02/82/19–20, 4 April 1982; one specimen, immature female, postrostral cl. 34.5 mm, AM P35488, Indian Ocean, north-west shelf of Australia, 220 km north-west of Port Hedland, 18°40'S, 116°44'E, 594–612 m, Engel trawl, J.R. Paxton on *Soela*, stn S02/82/28–30, 6–7 April 1982.

Remarks. The large ovigerous female is similar in size and form to the largest females of *C. suhmi* we have examined from the eastern coast of Australia. As in those specimens there is a spine between the protogastric spine and the anterior branchial spine and the surface of the carapace has only small, scattered granules. As well, the eyestalk is less than half the width of the orbit and the orbital width is clearly greater (1.5) than the interorbital width (measurements taken from above the eyestalk on the eave and the tip of the postorbital spine). The cornea is small. However, there is no spine on the posterior margin of the orbit, the anterior mesogastric tubercle is quite distinct and there is a narrow ridge between the female gonopore and the anterior margin of the segment which is lacking in eastern Australian specimens. The large protogastric spines and the rostral spines are all broken off not far above their bases in this specimen but the bases of the protogastric spines are directed straight forward.

The immature female (postrostral cl. 26.6 mm) from the Straits of Malacca is less than half the size of the ovigerous female, and in this specimen the postorbital spines are directed somewhat obliquely and the protogastric spines are slightly divergent. Oblique postorbital spines and slightly divergent protogastric spines have been reported in a number of juvenile *Cyrtomaia* specimens.

The immature female from the north-west shelf of Australia (postrostral cl. 34.5 mm) has long parallel protogastric spines but the rostral spines and interantennular spine are broken off, and it is infected

with a parasite in the left branchial region. In this specimen there is a high tubercle instead of a spine between the protogastric and anterior branchial spines, and the anterior mesogastric spine is smaller than in the other two specimens.

Cyrtomaia gaillardi Guinot & Richer de Forges from the western Indian Ocean differs from these specimens in having a carapace surface with larger and more dense granules.

These specimens are distinguished from *C. maccullochi* Rathbun by their smoother carapace, shorter eyestalk and much larger (more than one and a half times) adult size.

Distribution. Southern India, Bay of Bengal, Indonesia, north-western and eastern Australia, Japan.

Physachaeus Alcock

Type species. *Physachaeus ctenurus* Alcock, 1895, by subsequent designation of Griffin & Tranter, 1986.

Distribution. Indo-West Pacific.

Physachaeus ctenurus Alcock

Physachaeus ctenurus Alcock, 1895: 175–176, pl. 3 figs 2, 2a–b. — Griffin & Tranter, 1986: 42–44, figs 8, 15f, g.

Material examined. One specimen, ovigerous female, 9 mm, ZMC, Danish *Galathea* Deep Sea Expedition 1950–52, stn 490, Bali Sea, 5°25'S, 117°03'E, 600 m, sledge trawl, sand and clay, 14 September 1951.

Remarks. We have discussed recently (Griffin & Tranter, 1986: 43–44) the variation, within this species, based on specimens from the Andaman Sea, Philippines and Japan. This specimen from the Bali Sea agrees most closely with the specimen previously recorded from Mindanao (Griffin & Tranter, loc. cit). The rostral lobes are broad, triangular and apically acute with a V-shaped hiatus between them. The mesogastric spine is very much shorter than the cardiac spine and there is no low tubercle on the posterior cardiac slope. The basal antennal article is spinulose in the distal half and about five times as long as broad. The four spines on the abdomen are more pronounced than in the other specimens and the suture between the sixth and seventh segments is not visible even in the mid-line.

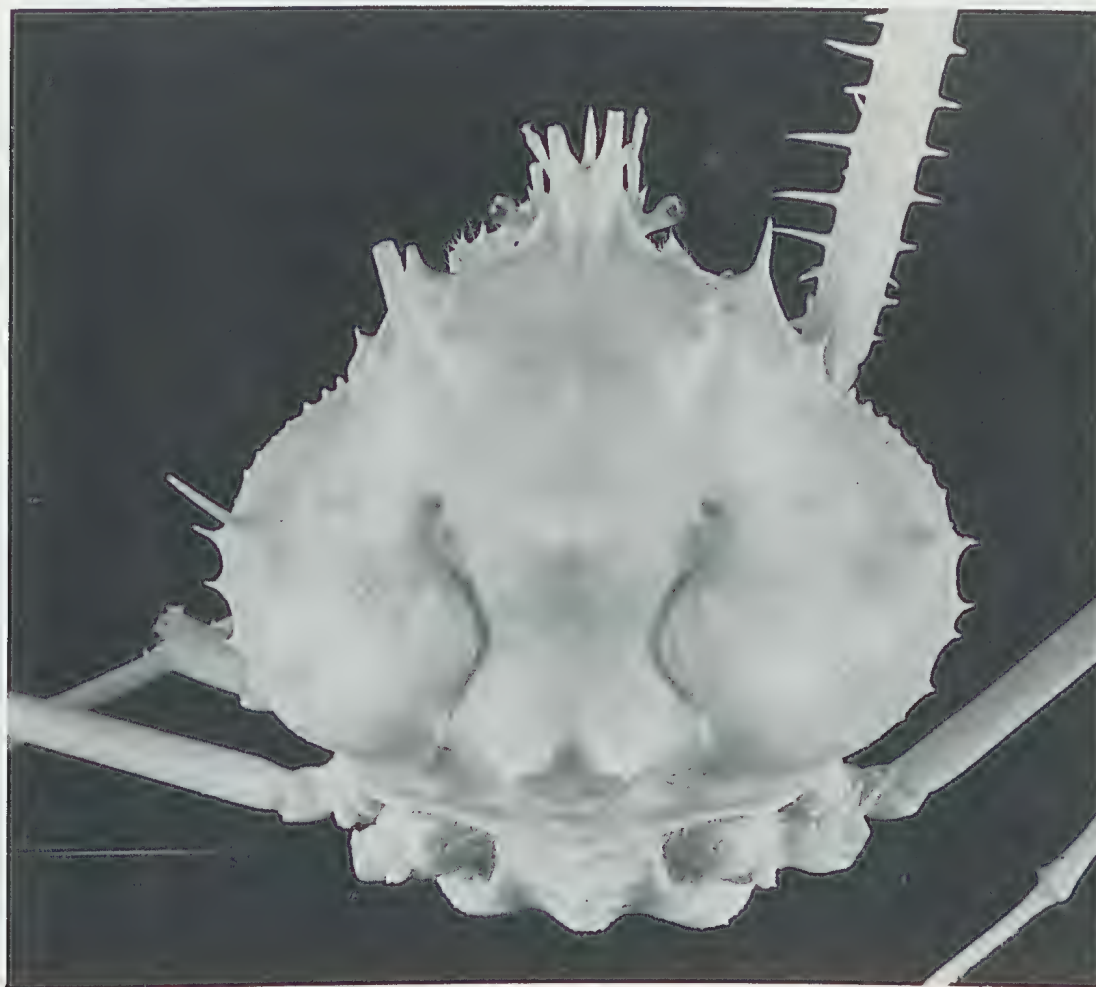


Fig. 1. *Cyrtomaia suhmi* Miers, ovigerous female, postrostral cl. 70 mm, Indian Ocean, north-west of Port Hedland, AM P35487, dorsal view of carapace.

Distribution. East Africa, south-west India, Andaman Sea, Nicobar Islands, Sumatra, Bali Sea, Philippine Islands, Japan.

Platymaia Miers

Type species. *Platymaia wyvillethomsoni* Miers, 1886, by monotypy.

Remarks. Previously only two species of *Platymaia* – *P. alcocki* Rathbun and *P. turbynei* Stebbing – had been reported from the Indian Ocean. We describe here a new species of *Platymaia* from off the north-west of Australia and also record *P. fimbriata* Rathbun, previously known only from the west Pacific, from the same area.

Distribution. Indo-West Pacific.

Platymaia fimbriata Rathbun

Platymaia fimbriata Rathbun, 1916: 531–532.—Griffin & Tranter, 1986: 46, fig. 10i, j.

Material examined. Three specimens, ovigerous females, 41 mm, 41 mm, 43 mm, AM P35492, Indian Ocean, north-west shelf of Australia, 250 km north-west of Port Hedland, 18°40'S, 116°42'E, 593 m, Engel trawl, J.R. Paxton on *Soela*, stn S02/82/19-20, 4 April 1982; one specimen, male, postrostral cl. 33 mm, AM P35491, Indian Ocean, north-west shelf of Australia, 250 km north-west of Port Hedland, 18°40'S, 116°30'E, 715 m, Engel trawl, J.R. Paxton on *Soela*, stn S02/82/22-24, 5 April 1982; two specimens, one male, 29.5 mm, one immature female, 29 mm, AM P35489, two specimens, male, 27.5 mm, 27.7 mm, AM P35490, Indian Ocean, north-west shelf of Australia, 220 km north-west of Port Hedland, 18°40'S, 116°44'E, 603 m, Engel trawl, J.R. Paxton on *Soela*, stn S02/82/28-30, 6–7 April 1982.

Remarks. These specimens agree with Rathbun's type series from the Philippine Islands in having a very spinulose carapace and in the presence of numerous spinules in irregular rows on the dorsal surface of the

third and fourth pairs of ambulatory legs. As noted previously (Griffin & Tranter, 1986) specimens of *P. fimbriata* from the Kai Islands and the Ceram Sea are as spinulose as the type series but, of the many specimens examined from off the northern coast of New South Wales, a large number are less spinulose. These specimens have only granules, or at most a row of very small spinules, on the dorsal surface of the last two pairs of ambulatory legs, and also many fewer carapace spines. We have not found any other difference which would justify regarding these smoother specimens as a separate species.

This is the first record of this species from the Indian Ocean.

Distribution. North-western and eastern Australia, Indonesia, Philippine Islands and Japan.

Platymaia mindirra n. sp.

Figs 3–8

Type material. Size range cl. 35 mm – postrostral cl. 85 mm. **HOLOTYPE:** male, postrostral cl. 78.7 mm, AM P35493, Indian Ocean, north-west shelf of Australia, 190 km north-west of Port Hedland, 18°16'S, 118°12'E, 300 m, Engel trawl, J.R. Paxton on *Soela*, stn S02/82/36, 10 April 1982. **PARATYPES:** one specimen, AM P35494, Indian Ocean, north-west shelf of Australia, east of Ashmore Is., 11°49'S, 124°17'E, 200 m, CSIRO *Courageous*, 10 June 1979; one specimen, AM P35497, Indian Ocean, north-west shelf of Australia, 190 km north-west of Port Hedland, 18°16'S, 118°12'E, 298–320 m, Engel trawl, J.R. Paxton on *Soela*, stn S02/82/36-37, 10 April 1982; two specimens, one male, one female, AM P35495, Indian Ocean, north-west shelf of Australia, 190 km north-west of Port Hedland, 18°16'S, 118°12'E, 298–320 m, Engel trawl, J.R. Paxton on *Soela*, stn S02/82/38, 11 April 1982; one specimen, immature male, 35 mm, AM P35496, Indian Ocean, north-west shelf of Australia, north-west of Port Hedland, 20°S, 117°40'E, about 40 m, fish trawl, *Soela*, 2–15 November 1983.

Description. Carapace subcircular, width almost



Fig. 2. *Cyrtomaia suhmi* Miers, ovigerous female, postrostral cl. 70 mm, Indian Ocean, north-west of Port Hedland, AM P35487, (left) lateral view of carapace, left side; (right) lateral view of carapace, right side.

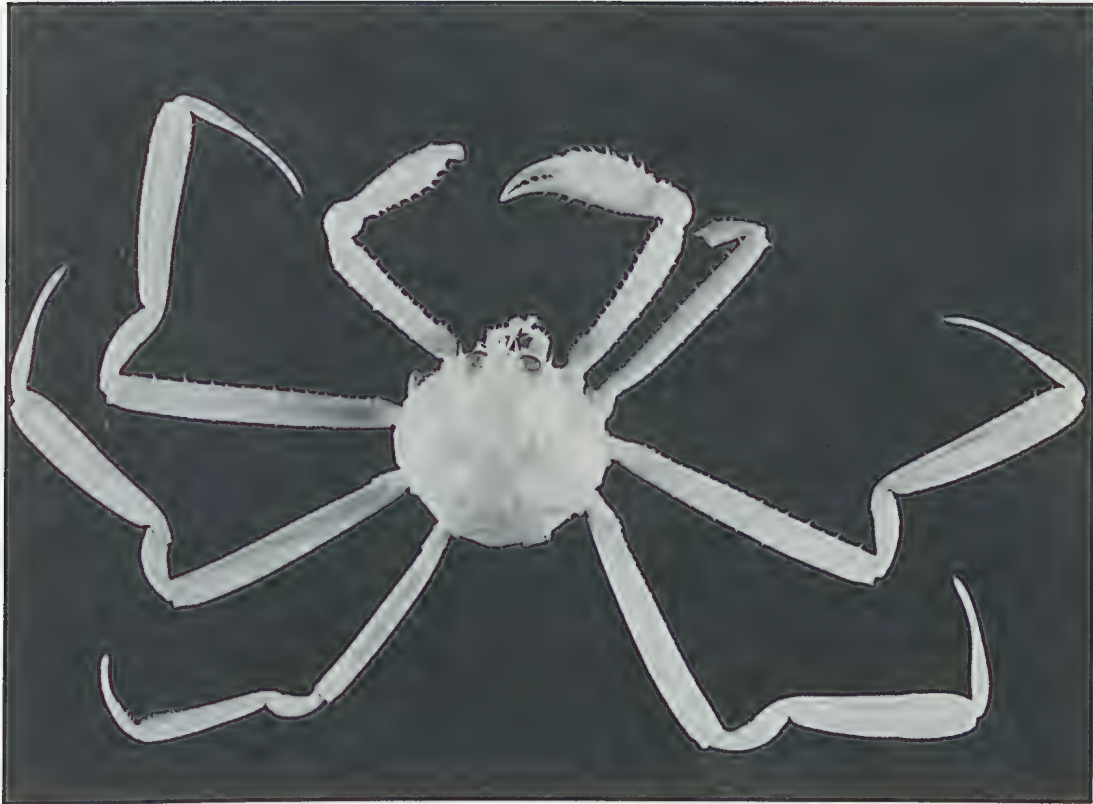


Fig. 3. *Platymaia mindirra*, holotype, male, postrostral cl. 78.7 mm, Indian Ocean, north-west of Port Hedland, AM P35493, dorsal view of whole animal.



Fig. 4. *Platymaia mindirra*, holotype, male, postrostral cl. 78.7 mm, Indian Ocean, north-west of Port Hedland, AM P35493, dorsal view of carapace.

equal (0.94–1.0) to postrostral carapace length; carapace surface with fine granules, lacking prominent dorsal tubercles or spines.

Rostral spines slender, directed upward and forward, subparallel or weakly divergent, length about one tenth (0.09–0.11) postrostral carapace length. Interantennular spine curved upward distally, length more than one and a half times rostral spines. Orbital eave narrow, sometimes with low tubercles; posterior margin of orbit smooth or with a low tubercle; postorbital spine slender, sharp, length about one third rostral spine.

Hepatic margin with a single spine, immediately ventral to postorbital spine and slightly longer. Branchial margin with 3 small tubercles close together anteriorly and 3 others well spaced along posterolateral margin.

Gastric regions strongly elevated, protogastric ridges weak and smooth; a pair of small, sharp, anterior protogastric tubercles, otherwise only very small mesogastric, metagastric and posterior protogastric tubercles, sometimes indistinct. Cardiac region slightly more elevated than branchial region, with a pair of broad, blunt, submedial tubercles. Intestinal region with a low central tubercle. Branchial regions smooth dorsally, only weakly elevated at anteromedial angle.

Basal antennal article slender, cylindrical, smooth except for 2 small tubercles in distal half; distal margin not quite reaching ventral lobe of front.

Epistome short; green gland adjacent to basal antennal article and anterolateral angle of mouthfield. Eyestalk short, cornea large, elongate, reaching postorbital spine; a small dorsal, subterminal tubercle. Pterygostomian region flat, smooth, margin with a short spine and 2–5 tubercles.

Third maxilliped merus narrower than ischium. Lateral margin of ischium with 3 small spines in distal half, a spinous ridge parallel and near to lateral margin; a row of spines near and parallel to mesial margin. Merus with anterolateral angle weakly produced and

bearing about 5 spines; a central row of 2–4 spines and 4–5 spines on the mesial margin. Exopod with a central, longitudinal row of spines. Palp inserted terminally.

First sternite of male sternum smooth with an anterior medial and a central spine; a pair of submedial spines behind central spine and a pair more widely spaced anterior to abdominal fossa, and another pair lateral to these last. Second sternite with 1 sharp tubercle and sternites 3 and 4 with 3 sharp tubercles on mesial half; sternites 2–4 each with 2 sharp tubercles on lateral margin.

Male abdomen of 7 free segments. Proximal width of third segment about one and a half times distal width, lateral margin convex proximally, nearly straight distally. Sixth segment as wide as long, width a little more than half (0.56) distal width of third segment. First segment with a row of 3 tubercles, segments 3 and 4 with a lateral tubercle near distal margin. Width of seventh segment about one and a third (1.3) times length.

First pleopod of male straight, curving outwards at the apex, aperture medial, just behind apex.

Female abdomen of 7 free segments; first segment with 3 tubercles, second with a ridge bearing 6 six small tubercles; segments 3–6 with a pair of distal, submedial tubercles or spines, seventh segment with a central pair of submedial spines; some spines laterally on segments 3–7. Female gonopore opening mesially.

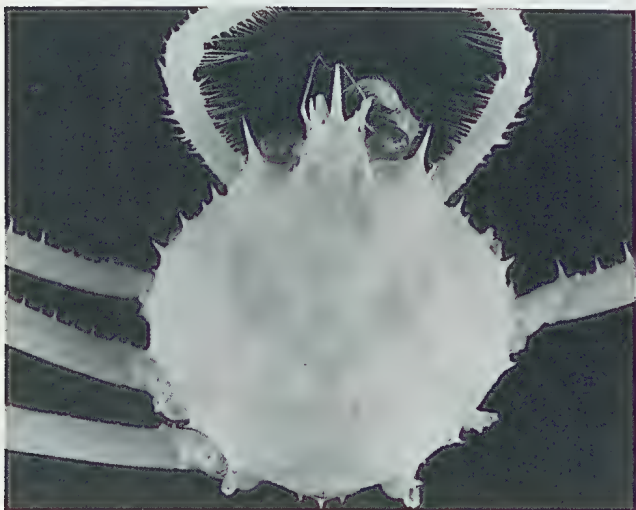


Fig. 5. *Platymaia mindirra*, paratype, immature male, cl. 35 mm, Western Australia, AM P35496, dorsal view of carapace.



Fig. 6. *Platymaia mindirra*, holotype, male, postrostral cl. 78.7 mm, Indian Ocean, north-west of Port Hedland, AM P35493, male abdomen.

Cheliped of male about one and three quarters times (1.8) postrostral carapace length. First ambulatory leg length more than three and a half times (3.7–4.7) postrostral carapace length, relatively longer in larger specimens. Fourth ambulatory leg 3 times postrostral carapace length. Cheliped merus of male with 7 short, well spaced spines on dorsal margin; inner and outer ventral margins with double rows of longer, more closely spaced spines and a longitudinal row of 9 short spines midway along inner face. Carpus with a few small spines. Cheliped palm with a row of long spines on dorsal margin, a double row of spines on ventral margin, a longitudinal row of short spines midway along inner face and a longitudinal row of very small spines midway along outer face. Fingers more than two thirds (0.7) length of palm; dactyl with 1 or 2 proximal, dorsal spines. A moderate gape between fingers in proximal three quarters with 3–4 large teeth on each finger in the gape and a few small teeth distally.

First ambulatory leg with spines on both margins of merus, carpus, propod and dactyl. Second ambulatory leg with spines on both margins of merus and propod and posterior margin of dactyl; third ambulatory leg with spines only on anterior margin of merus and fourth leg without marginal spines. All ambulatory legs smooth dorsally. Propodi of ambulatory legs 2–4 markedly compressed and broadened, length 4–5 times width; dactyl also compressed, distal half much narrower than proximal half, terminally sharp.

Remarks. This new species is similar to other species of *Platymaia* which have a broad carapace without dorsal spines, i.e. *P. bartschi* Rathbun, *P. maoria* Dell and *P. wyvillethomsoni* Miers from the western Pacific and *P. alcocki* Rathbun from the Indian Ocean. It is distinguished from all these species by the very broad propod of the second to fourth pairs of ambulatory legs. The width of the propod of the second ambulatory leg in *P. mindirra* is a quarter to a fifth the length while in *P. alcocki* the width is less than one seventh the

length. In the other three species mentioned above, the width is less than one eighth the length.

As well, this series of specimens seems to indicate that this species is larger at maturity than other known species of *Platymaia*. The postrostral carapace length of *P. mindirra* is nearly one and a half times that of adult *P. bartschi*.

The smooth protogastric ridges distinguish this species from *P. wyvillethomsoni* and *P. alcocki* in which the ridges are tuberculate. This species is distinguished from *P. maoria* by the presence of three tubercles on the first segment of the male abdomen, rather than one, and by the absence of the transverse row of three spines present on the gastric region of *P. maoria*.

This species is similar to *P. bartschi* in smoothness of carapace, the length of the rostral, interantennular and postorbital spines and shape of the first pleopod of the male. It can be distinguished from *P. bartschi* by several features apart from the broader ambulatory legs and larger size. In *P. mindirra* the mesogastric tubercles are hardly raised above the surface and are often indistinct while in *P. bartschi* these tubercles, though small, are quite distinct. The carapace surface in *P. mindirra* is covered with fine granules and the first segment of the male abdomen is smooth but in *P. bartschi* both the carapace and first segment of the male abdomen are covered with coarse granules. The dactyls of ambulatory legs two to four in *P. mindirra* are broad at the base, then uniformly narrow distally, but in *P. bartschi* after the dactyl narrows it widens slightly before the apex.

The young male (35 mm) in our series has small carapace spines on the gastric regions and branchial margins which are not present in the adults. We have compared this specimen with an immature specimen of *P. alcocki* of similar size (AM G1476, 30 mm) and they differ in several features. On the posterior hepatic region and the anteromedial branchial region there is a tubercle in young *P. mindirra*, whereas in young *P. alcocki* there are well developed spines in these positions. As well, in young *P. mindirra* the carapace surface is finely granular (coarsely granular in *P. alcocki*); the interantennular spine is one and a half times the rostral spines (subequal in *P. alcocki*) and the length of the propod of the fourth ambulatory leg is five and a half times the width (seven and a half times in *P. alcocki*).

Adult and subadult specimens of *P. turbynei* Stebbing are similar in size to this young specimen of *P. mindirra* but they have a much narrower propod (i.e. length about 20 times width); the anterior protogastric spines are much closer to the midline than are the posterior protogastrics; and the carapace surface is smooth between the spines whereas in *P. mindirra* it is finely granular.

Etymology. The species takes its name from the aboriginal name for crab (*mindirra*) used by the Payungu language group of the north-west coast of Australia. Mr Nicholas Reid of the Australian Institute



Fig. 7. *Platymaia mindirra*, holotype, male, postrostral cl. 78.7 mm, Indian Ocean, north-west of Port Hedland, AM P35493, male right chela, outer view.

of Aboriginal Studies kindly provided information about the Payungu language.

Distribution. Indian Ocean, off Western Australia from 11°49'S, 124°17'E to 20°S, 117°40'E.

Platymaia turbynei Stebbing

Platymaia turbynei Stebbing, 1902: 3–5, pl. 5.—Barnard, 1950: 31–32, 816 (in part), figs 6a–c; Griffin, 1974: 27; Crosnier, 1976: 241–242; Kensley, 1977b: 183, fig. 16.

Material examined. Four specimens, one male, 40 mm, one ovigerous female, 40.5 mm, two juveniles, 5 mm, 6.5 mm, ZMC, Danish *Galathea* Deep Sea Expedition, stn 202, off Natal, 25°20'S, 35°17'E, 630 m, grab, sand, 21 February 1951; fourteen specimens, one male, 39.4 mm, one ovigerous female, 39.3 mm, seven males, 9.2–14.5 mm, five females, 9.3–14.0 mm, Danish *Galathea* Deep Sea Expedition, stn 203,

off Natal, 25°36'S, 35°21'E, 730 m, otter trawl, 21 February 1951.

Remarks. In this species there are 13 prominent dorsal carapace spines (4 protogastric, 2 mesogastric, 2 cardiac, 4 branchial, 1 intestinal) and the carapace surface is smooth between them; the short postorbital spine is only about a quarter the length of the rostral spines; the carapace width is slightly less (0.87–0.97 in this series) than the postrostral carapace length; the propodi and meri of ambulatory legs two to four are subequal in length and the dactyls are not broadened before the tip.

In a male (40 mm) in this series the cheliped palm is about one and a half (1.4) times as long as high, and the fingers are shorter (0.85) than the palm.

The two ovigerous females (39.3, 40.5 mm) are slightly smaller than the ovigerous females (44–47 mm) in the collection reported by Kensley (1977b).

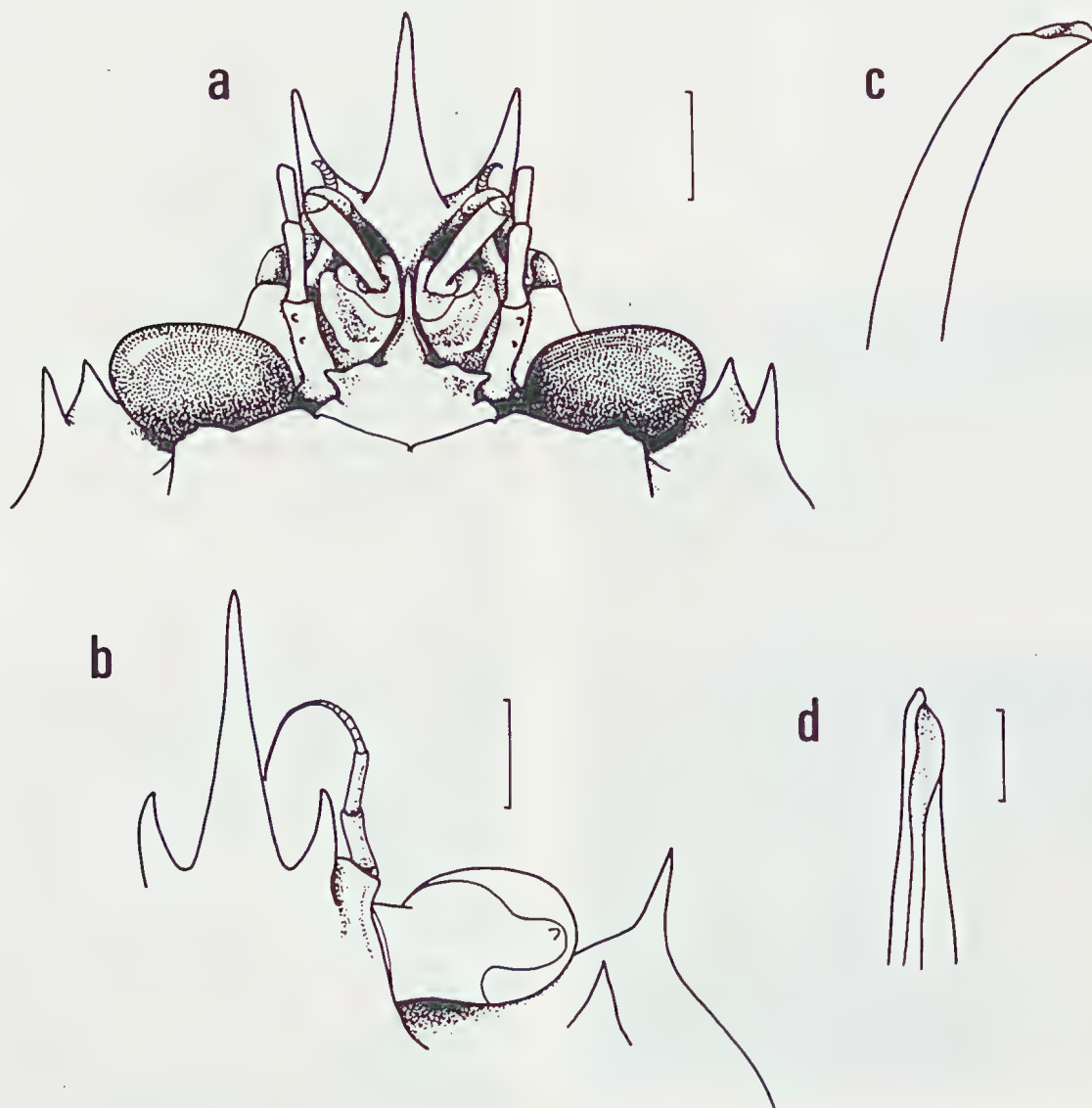


Fig. 8. *Platymaia mindirra*, holotype, male, postrostral cl. 78.7 mm, Indian Ocean, north-west of Port Hedland, AM P34593: a, ventral view of orbits; b, dorsal view of right orbit; c, abdominal view of first left pleopod; d, sternal tip of first left pleopod. Lines of scale a and b represent 5 mm, d represents 1 mm.

As noted by Crosnier (1976: 242) the specimen (male, cl. 45 mm) reported by Barnard (1950: 816) is not *P. turbynei* but an immature specimen of *P. alcocki* Rathbun.

Distribution. East coast of South Africa from Natal to southern Mozambique Channel, Madagascar, La Réunion.

Pleistacantha Miers

Type species. *Pleistacantha sanctijohannis* Miers, 1879, by monotypy.

Remarks. Considerable controversy has surrounded several species of this genus. The present study attempts again to clarify the status of *P. moseleyi*.

Distribution. Indo-West Pacific.

Pleistacantha moseleyi (Miers)

Figs 9a, 10a

Echinoplax moseleyi Miers, 1886: 32–33, pl. 4 fig. 2.

Echinoplax pungens Wood-Mason in Wood-Mason & Alcock, 1891: 259.—Alcock, 1895: 179; Alcock & Anderson, 1896: pl. 17 fig. 1, pl. 39 fig. 1.

Pleistacantha moseleyi.—Doflein, 1904: 76–78, pl. 24 figs 5, 6, pl. 25, pl. 26; Stebbing, 1923: 2; Barnard, 1950: 34–35, fig. 6c; Grindley, 1961: 127–128, fig. 1; Sakai, 1965: 70 (in discussion), fig. 10c; Berry & Hartnoll, 1970: 213–215, pl. 1; Griffin, 1974: 27–28; 1976: 208; Guinot & Richer de Forges, 1982a: 1102–1105, fig. 6C, D, pl. 3 fig. 3; Griffin & Tranter, 1986: 49, 51, 52 (in discussion).

?*Pleistacantha pungens*.—Guinot & Richer de Forges, 1982a: 1110–1112, figs 6A, B, 8A–A2, pl. 3 figs 2, 2a.

Material examined. One specimen, female, 87 mm, ZMC, Danish *Galathea* Deep Sea Expedition, stn 436, Philippine Islands, east of Cebu, 10°12'N, 124°14'E, 710 m, trawl &

dredge, green mud, 9 August 1951; one specimen, male, 69 mm, AM G1475, (exchange from Indian Museum, Calcutta, 1897), Andaman Sea, 234–450 m; two specimens, one male, postrostral cl. 60 mm, one female, 76.5 mm, AM P35498, Indian Ocean, north-west shelf of Australia, 18°33'S, 117°31'E, 400 m, *Soela*, 25 April 1983; one specimen, female, 61.8 mm, AM P35499, Western Australia, 20°S, 117°40'E, about 40 m, fish trawl, *Soela*, 2–15 November 1983.

Remarks. This species has been discussed recently by Guinot & Richer de Forges (1982a) and Griffin & Tranter (1986). There is disagreement as to how many species there are. We still see no reason to remove *P. pungens* from synonymy with *P. moseleyi* as Guinot & Richer de Forges suggest.

Guinot & Richer de Forges have raised several questions in discussion which may be summarised as follows:

1. Is the type of *P. moseleyi* a juvenile of *P. pungens* from the Andaman Sea?

2. Are the small specimens from east Africa reported by Doflein as *P. moseleyi* (a) juveniles of the large specimens from South Africa reported as *P. moseleyi* by Stebbing (1923), Barnard (1950), Grindley (1961) and Berry & Hartnoll (1970); (b) juveniles of the large specimens from Nicobar Islands and off Sumatra discussed by Doflein; (c) conspecific with the type of *P. moseleyi* from the Philippines but not growing to a large adult of more than 80 mm carapace length?

3. Are the large males from Malagasy (Guinot & Richer de Forges, 1982a) conspecific with the large specimens discussed by the South African authors?

4. Are either or both 2 and 3 (above) conspecific with the large specimens from the Andaman Sea and eastern Indian Ocean reported by Wood-Mason & Doflein, and those from the Philippines reported by Griffin (1976)?

Doflein (1904) considered *P. pungens* (Wood-Mason,

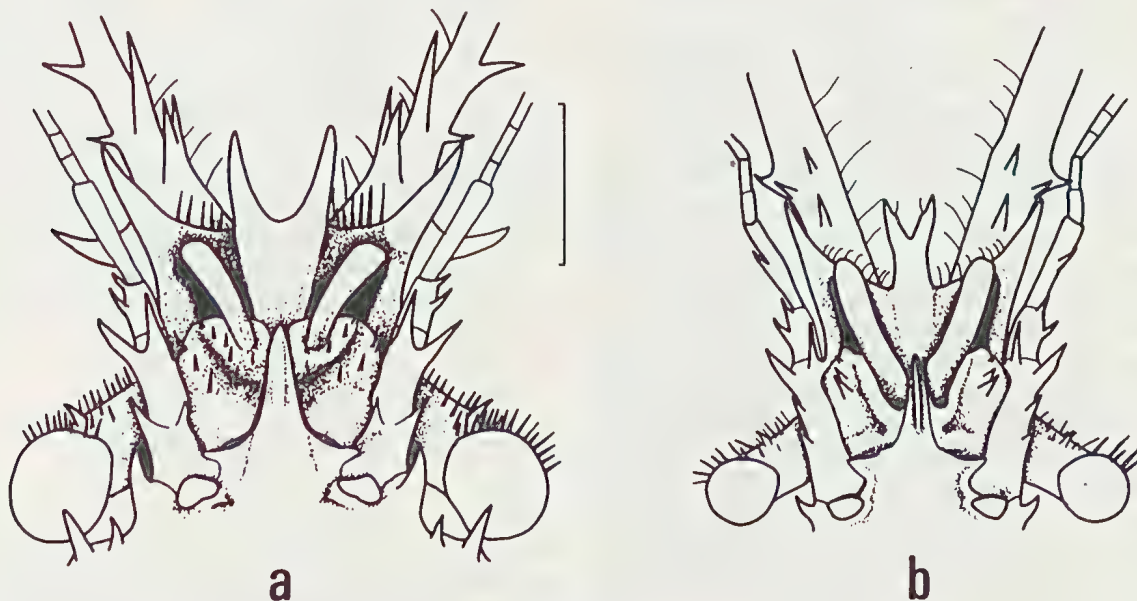


Fig. 9. Posteroventral view of interantennular spine of: a, *Pleistacantha moseleyi* (Miers), male, cl. 69 mm, Andaman Sea, AM G1475; b, *Pleistacantha oryx* Ortmann, male, cl. 40.5 mm, Sagami Sea, Japan, AM P34571. Lines of scale represent 1 mm.

1891) from the Andaman Sea to be a synonym of *P. moseleyi* (Miers, 1886) from the Philippines. The holotype of *P. moseleyi* is an immature female (15 mm) while the type material of *P. pungens* includes large adult specimens (to 88 mm). At the same time Doflein identified both the juvenile specimens from off Dar-es-Salaam and sub-adult and adult specimens from the eastern Indian Ocean, collected by the *Valdivia*, as *P. moseleyi*.

Guinot & Richer de Forges have questioned Doflein's decisions. They have examined the holotype of *P. moseleyi* but not any specimens from the Andaman Sea identified as *P. pungens*. They have identified as *?P. pungens* three large males recently collected off Malagasy.

The discovery of small but adult specimens with the large eyes and the distally smooth rostral spines of the holotype of *P. moseleyi* would justify the separation of *P. moseleyi* and *P. pungens* again. On the other hand, the series of specimens from the Philippines reported by Griffin (1976) which ranged in size from 20 mm to 97 mm supports the idea that the holotype of *P. moseleyi* is a juvenile of a large species and that the differences noted between the two by Wood-Mason and by Guinot & Richer de Forges are related to the great difference in size between the juvenile and adult in this species. For if the type of *P. moseleyi* (15 mm) is an immature female of a species which has a carapace length of 80–90 mm when adult then it could be expected to differ in a number of respects. Several of the differences noted by Wood-Mason between *P. moseleyi* and *P. pungens* – larger size, smaller eyes, more pyriform carapace, thicker legs and broader abdomen of the female – would be accounted for by *P. moseleyi* being a juvenile and not an adult female as Miers had stated. (In other species of majids, eg. *Paranaxia serpulifera*, juvenile specimens of only 15–30 mm are collected, while the adult reaches a carapace length of more than 120 mm.)

There is confusion about the degree to which the interantennular spine is divided in the various specimens which have been reported. It seems important to us to consider the degree to which the interantennular spine tapers along its length as well as the proportion which is bifid. Our series of specimens includes a large adult female (cl. 87 mm) from the same general area as the type locality of *P. moseleyi* (Philippine Islands) and a male (69 mm) from the Andaman Sea (AM G1475, exchange from the Indian Museum), the type locality of *P. pungens*. This specimen from the Andaman Sea has the interantennular spine divided for at least the distal half (Fig. 9a), though this seems to disagree with the remark made by Sakai (1976: 174) that in another specimen he examined from the Andaman Sea the interantennular spine was bifid only at the tip. In all the specimens of this series the interantennular spine has the same form and this seems, from Guinot & Richer de Forges' figure, to be similar to *?P. pungens* from Malagasy. We have also figured the interantennular spine of *P. oryx* for comparison (Fig. 9b).

Guinot & Richer de Forges remark that their specimens of *?P. pungens* have more accessory spines on the rostral spines than does the typical *P. pungens* of Wood-Mason. In our series of specimens some of the rostral spines are broken, but on those which are complete there are three to six lateral spines and three ventral spines on the rostral spines beyond the fused base. On two of the specimens there is one dorsal accessory spine. The specimen figured by Guinot & Richer de Forges appears to have five to six lateral spines, three ventral and one to two dorsal spines.

Neither of our male specimens (69 mm and postrostral cl. 60 mm) has enlarged chelae and both have the rostral spines straight and divergent from the base, not tending to be subparallel distally as in adult males.

The first pleopod of the males in our series is not so strongly curved outwards at the tip as in the specimens figured by Guinot & Richer de Forges, and the sub-terminal 'spine' is at right angles to the surface of the pleopod (Fig. 10a). The specimen of *?P. pungens* figured by Guinot & Richer de Forges has only a small spinule among the stiff setae on the eyestalk. In the specimens in our series there is an antero-ventral spine, which is sometimes short, and in two specimens there is a short, slender terminal spine above the cornea. These differences between the specimens described as *?P. pungens* and our series of *P. moseleyi* seem slight. It is possible, however, that the examination of further specimens will show that they, and perhaps the other large specimens from South Africa, are a new species distinct from *P. moseleyi*. If this were so then it is possible that the small specimens from east Africa, described by Doflein, could be the juveniles of this

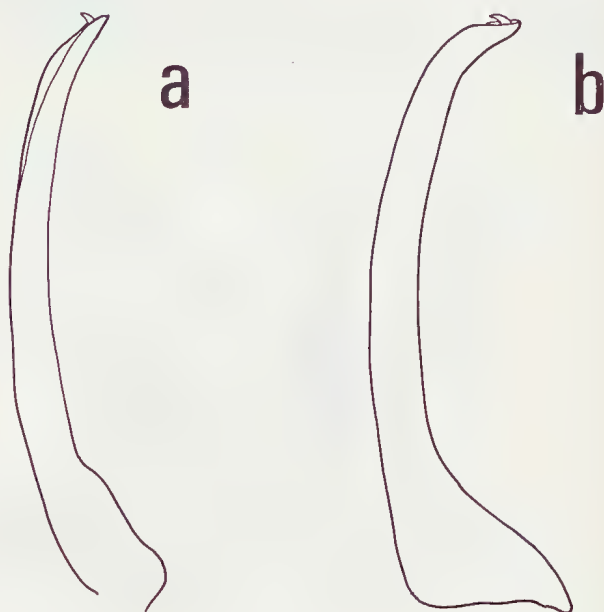


Fig. 10. Left first pleopod of male of: a, *Pleistacantha moseleyi* (Miers), cl. 69 mm, Andaman Sea, AM G1475; b, *?P. pungens*, cl. 83 mm, Madagascar, MP-B7274 (after Guinot & Richer de Forges, 1982a: fig. 8A).

species. These juveniles are at present regarded as being conspecific with the type of *P. moseleyi*. However, there is no evidence to suggest that these juveniles, with the type, represent a distinct species of which the adult remains unknown.

The arguments advanced by Guinot & Richer de Forges are not supported by the available evidence and we maintain our opinion that all the specimens from the Pacific, and the east and west Indian Oceans as well, are the single species *P. moseleyi*: we reflect this in the synonymy.

The record of this species from off northern Western Australia extends its known range considerably further south in the eastern Indian Ocean.

Distribution. Widespread Indo-West Pacific: South Africa, east Africa, Malagasy, Andaman Sea, Great Nicobars, Nias, north Western Australia, Philippine Islands.

Subfamily PISINAE

Rochinia A. Milne Edwards

Type species. *Rochinia gracilipes* A. Milne Edwards, 1875, by monotypy.

Remarks. Three new species are described here. This genus now contains 32 Indo-West Pacific species, a third of these (11) having been described since 1973. Many of these are from deep water and it seems probable that many species still await discovery. Often only a few specimens are collected, as with the new species described here, and there is a reluctance to base a new species on such a small amount of material. This tendency can lead to some confusion, as for example in the case of *Rochinia riversandersoni* (Alcock), and we discuss this in detail under *R. sibogae*.

A key to this genus was published recently (Griffin & Tranter, 1986). This key needs to be adapted to accommodate the three new species described here and also the probable new species which have been previously included in *R. riversandersoni*. These changes are discussed under *R. sibogae* and *R. soela*.

Distribution. Indo-West Pacific, Atlantic and east Pacific.

Rochinia galathea n. sp.

Fig. 11

Type material. HOLOTYPE: male, postrostral cl. 9.2 mm, ZMC, Indian Ocean, off Natal, 25°20'S, 35°17'E, 535–610 m, sand, sledge trawl, otter trawl, Danish *Galathea* Deep-Sea Expedition, stn 202, 21 February 1951.

Description. Carapace broadly pyriform, width more than two thirds (0.7) postrostral carapace length; surface with a thick tomentum and several slender spines.

Rostral spines slender, straight, weakly divergent, fused basally; length greater than one third postrostral

carapace length (tip broken on one remaining rostral spine).

Orbital eave moderately expanded; a slender, sharp, preorbital spine directed forwards and slightly upwards; postorbital lobe separated from eave by a broad U-shaped hiatus; postorbital lobe short, laterally flattened, elongate in lateral view, separate from large hepatic lobe. Eyestalks short, slender; cornea terminal.

Hepatic margin not elevated; a large laterally flattened hepatic lobe, directed dorsally with apex curving over dorsal surface, height twice width, apically sharp. Lateral faces of postorbital and hepatic lobes flattened and polished.

Branchial submargin with 2 tubercles, the posterior one smaller; a prominent epibranchial spine, directed laterally and slightly upwards, in length about two fifths (0.39) carapace width.

Gastric regions weakly elevated; a slender, sharp metagastric spine; a small, low, protogastric tubercle anterolateral to spine. Cardiac region with a slender, sharp spine, about two thirds length of epibranchial spine. Branchial region anteriorly and posteriorly with a slender, sharp spine subequal to metagastric and slightly shorter than cardiac spine. Intestinal region with a slender medial spine near posterior carapace margin, as long as branchial spines. The 6 equidistant, subequal, slender spines on gastric, branchial and intestinal regions surround central cardiac spine.

Basal antennal article smooth, slightly depressed centrally; anterolateral angle produced forward into a very short, blunt tubercle; lateral margin very weakly concave; medial margin concave, produced slightly over antennal fossa; a tubercle lateral to green gland.

Pterygostomian region smooth, margin with 2–3 broad tubercles, tending to unite to form a tuberculate ridge. Third maxilliped smooth, anterolateral angle of merus moderately produced and rounded.

Cheliped of male about one and a third (1.3) times postrostral carapace length; merus smooth, trigonal, carinate on dorsal and outer ventral edges, inner ventral edge sharp; dorsal carina having a small, sharp, proximal lobe, with a rounded lobe just in front of it, and a short blunt terminal lobe; outer ventral carina with several small lobes along its length. Carpus smooth with a carinate ridge dorsally and a smaller carina on inner ventral edge. Chela with palm about one and a half (1.6) times long as high, dorsal margin carinate, ventral margin sharp; fingers nearly as long as (0.9) palm, low teeth along cutting edge of both fingers, narrow gap between fingers in proximal half.

Ambulatory legs smooth, slender, meri each with a short, conical terminal spine; dactyl of fourth leg with about 12 small teeth ventrally along its length; first leg about twice postrostral carapace length; fourth leg about half (0.55) length of first leg.

Male sternum smooth. Male abdomen of 7 free segments, smooth; third segment more than one and a half times (1.7) wider than sixth segment; sixth segment one and a half times (1.6) wide as long; seventh segment wide as long, broadly convex on terminal margin.

First pleopod of male straight, broad, apex truncate, medially rounded, laterally subacute; aperture appears to be terminal.

Remarks. This species has in common with *Rochinia riversandersoni* (Alcock) a cardiac spine surrounded by six other spines and a pair of long epibranchial spines. It is distinguished from *R. riversandersoni* by the very broad hepatic lobe, half as wide as high and tapering only near the tip. This petaloid hepatic lobe curves

medially over the dorsal surface of the carapace. Doflein (1904) figured specimens of *R. riversandersoni* from off Somalia which have a distally slender hepatic spine directed dorsolaterally.

Rochinia galathea is distinguished from *R. natalensis* Kensley by the broad hepatic lobe and by the presence of only one spine (mesogastric) on the gastric region, while in *R. natalensis* there are four spines (two mesogastric and a pair of proto gastric spines).

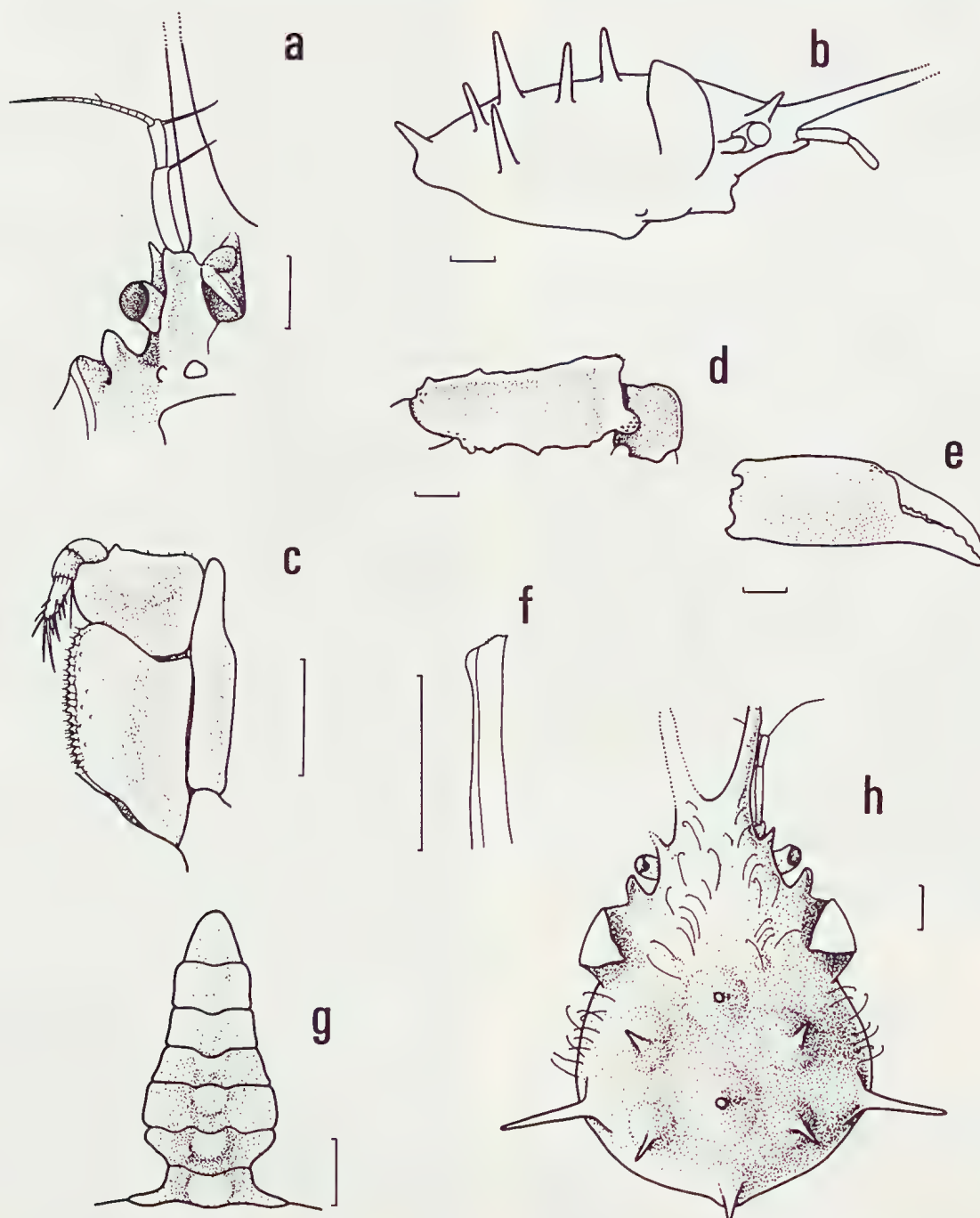


Fig. 11. *Rochinia galathea*, holotype, male, postrostral cl. 9.2 mm, off Natal, ZMC: a, right orbit, ventral view; b, carapace, lateral view; c, left third maxilliped; d, right cheliped, merus and carpus; e, right chela; f, left first pleopod, abdominal view; g, abdomen; h, carapace, dorsal view. Lines of scale represent 1 mm.

Etymology. The species is named for the Danish research vessel *Galathea*.

Distribution. Known only from the type locality, off Natal.

Rochinia luzonica (Rathbun)

Sphenocarcinus luzonicus Rathbun, 1916:539–540.—Griffin, 1976: 211–213, fig. 11a.

Rochinia luzonica.—Griffin & Tranter, 1986: 180, fig. 63c, d.

Material examined. One specimen, male, 39.3 mm, ZMC, Philippine Islands, off Mindoro, 13°07'N, 120°52'E, ca. 525 m, from the cable, stones and mud, 10 May 1930.

Remarks. In this adult male the rostral spines are strongly divergent in the distal half and also curved upward slightly; their length is 0.8 postrostral carapace length. The cardiac plate is transversely elongate (width = 1.5 x length) rather than subcircular as in specimens previously examined. In *R. stimpsoni* the width of the cardiac plate is more than twice the length.

Distribution. Indonesia, Philippine Islands.

Rochinia mosaica (Whitelegge)

Pugettia mosaica Whitelegge, 1900: 141–142, pl. 35 figs 5, 6, 7.—Griffin, 1972: 70–71.

Doclea profunda Rathbun, 1918: 16–17, pl. 7 figs 1, 2.—Hale, 1927: 134, fig. 134.

Rochinia mosaica.—Griffin & Tranter 1986: 185, figs 58, 62e, f.

Material examined. Three specimens, females, 7 mm, 9.1 mm, 8.5 mm, AM P35503, Tasman Sea, east of Sydney, 34°11.1'S, 151°26'E, 198–191 m, R. Springthorpe on *Tangaroa*, stn U207, 5 October 1982; one specimen, male, 7.6 mm, AM P35502, Tasman Sea, east of Sydney, 34°13.8'S, 151°29.1'E, 498–466 m, R. Springthorpe on *Tangaroa*, stn U208, 5 October 1982.

Remarks. These specimens agree with those previously reported.

Distribution. South-east and southern Australia from Cape Moreton (Queensland) to the Great Australian Bight (South Australia).

Rochinia pulchra (Miers)

Anamathia pulchra Miers, 1886: 26–27, pl. 4 figs 1, 1a–c. *Scyramathia pulchra*.—Alcock, 1895: 202–203.—Doflein, 1904: 84, pl. 27 fig. 12.

Rochinia pulchra.—Sakai, 1938: 278–279, fig. 35, pl. 37 fig. 4; 1976: 223–224, pl. 79 fig. 1; Griffin & Tranter, 1986: 185–187.

Material examined. One specimen, ovigerous female, 43.6 mm, AM P35501, Indian Ocean, north-west shelf of Australia, 240 km north-west of Port Hedland, 18°06'S, 117°45'E, 500 m, Engel trawl, J.R. Paxton on *Soela*, stn S02/82/31, 7 April 1982.

Remarks. This specimen agrees with others previously reported. The cardiac, epibranchial and dorsal branchial spines are curved slightly forwards. There is a pair of short, submedial spines just behind the anterior mesogastric spine.

This species has not been recorded from Australia before.

Distribution. Indo-West Pacific from east Africa to Philippines and Japan.

Rochinia sibogae n. sp.

Fig. 12

Type material. HOLOTYPE: female, ovigerous, postrostral cl. 11.0 mm, ZMA, Ceram Sea, east of Ceram, 3°37.7'S, 131°26.4'E, 924 m, fine grey mud, deep-sea trawl, 26 August 1899, *Siboga*, stn 170. PARATYPE: female, immature, postrostral cl. 8.5 mm (damaged), ZMA, as for holotype.

Description. Carapace broadly pyriform, width more than two thirds (0.73) postrostral carapace length; surface smooth with spines and a few low tubercles.

Rostral spines slender, straight, strongly divergent; length greater than half postrostral carapace length (tips broken); fused basally.

Orbital cave moderately expanded; a blunt, laterally flattened preorbital lobe, directed forwards and slightly upwards; postorbital lobe separated from cave by a broad U-shaped hiatus; postorbital lobe short, laterally flattened, continuous posteriorly with hepatic lobe. Eyestalks short, slender; cornea terminal.

Hepatic margin not elevated, a large laterally flattened hepatic lobe, directed dorsally, more than twice as high as wide, apically rounded and anteriorly continuous with postorbital lobe. Lateral faces of preorbital, postorbital and hepatic lobes flattened and polished.

Branchial submargin with a low tubercle; a long slender epibranchial spine directed upwards as well as laterally, nearly as long as carapace is wide.

Gastric regions elevated, a blunt metagastric tubercle; a smaller, low, protogastric tubercle anterolateral to metagastric. Cardiac region with a blunt spine, less than a third length of epibranchial spine. Branchial region with a small, blunt anterior tubercle and a smaller tubercle posterolateral to cardiac spine. Intestinal region with a strong, blunt, medial spine near posterior carapace margin, about two thirds length of cardiac spine.

Basal antennal article smooth, a shallow central groove along its length; anterolateral angle produced forward into a short, blunt tubercle; lateral margin straight; medial margin concave, produced slightly over antennal fossa; a tubercle lateral to green gland.

Pterygostomian region smooth, margin with 3 tubercles. Third maxilliped smooth, anterolateral angle of merus moderately produced and rounded.

Cheliped of female slightly longer (1.16) than postrostral carapace length; merus smooth, trigonal,

dorsal carina with large proximal lobe, a smaller lobe at proximal third and a prominent terminal spine; carpus smooth with a carinate ridge dorsally; palm about twice as long as high, margins not carinate; fingers a little shorter than palm, low teeth along all of cutting edge of both fingers.

Ambulatory legs smooth, slender, meri with a short broad terminal spine; dactyl of fourth leg with a few very small teeth amongst tomentum ventrally along its length; fourth leg about one and a quarter times postrostral carapace length. (Only chelipeds and the

third and fourth ambulatory legs on right hand side still attached to specimen.)

Female sternum smooth, first sternite with a shallow depression centrally. Female abdomen of 7 free segments, smooth, covered with tomentum, a low medial ridge on segments 1-4. Female gonopore a simple subcircular aperture, opening ventrally.

Smaller specimen, an immature female, damaged anteriorly. Preorbital and hepatic lobes apically subacute; epibranchial spines very slender, length about two thirds (0.65) carapace width. Cardiac spine just

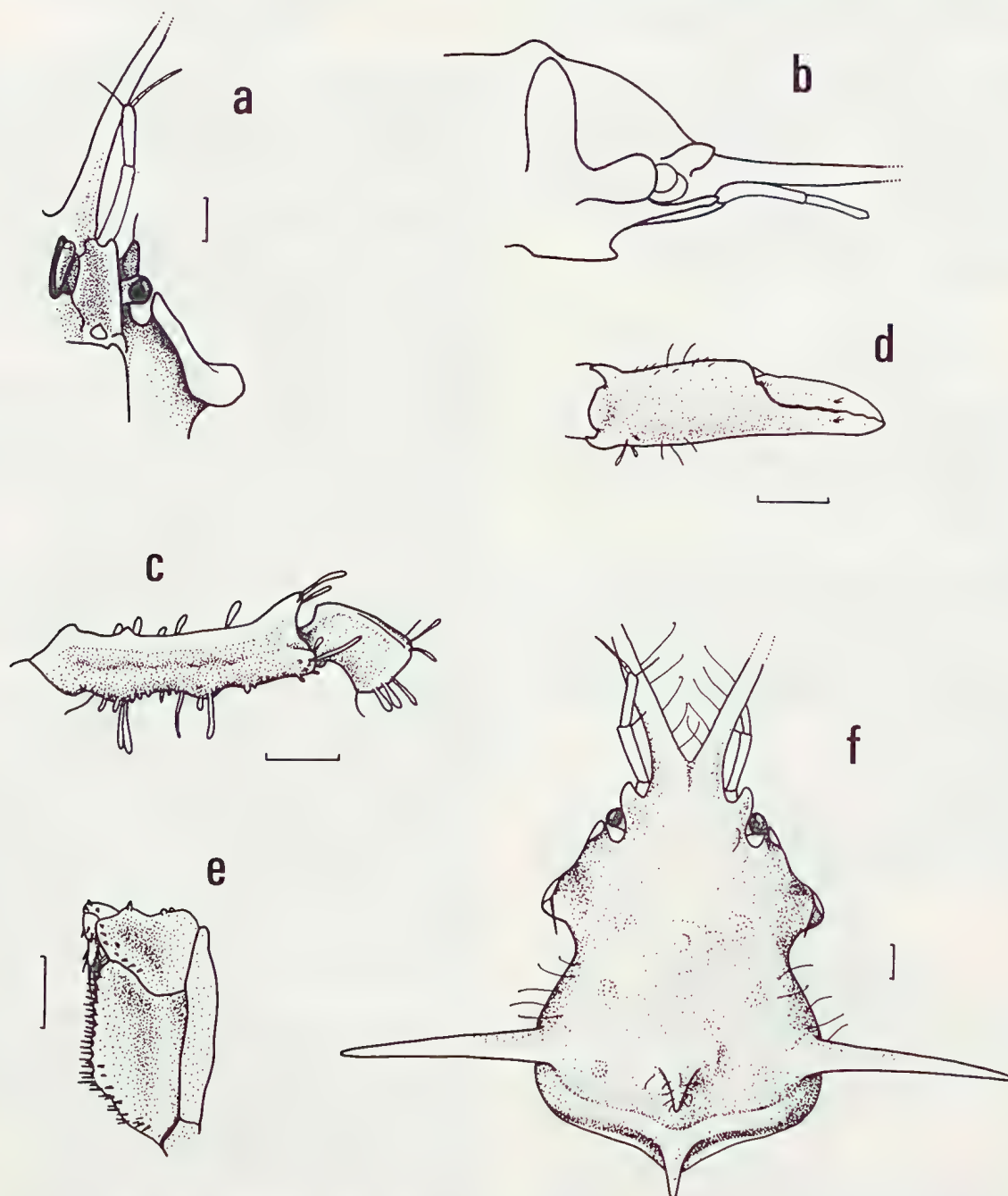


Fig. 12. *Rochinia sibogae*, holotype, ovigerous female, postrostral cl. 11.0 mm, Ceram Sea, ZMA: a, left orbit, ventral view; b, right anterior carapace, lateral view; c, right cheliped merus and carpus; d, right chela; e, left third maxilliped; f, carapace, dorsal view. Lines of scale represent 1 mm.

showing above tomentum and intestinal region with a tubercle concealed in tomentum rather than a spine as in adult.

Remarks. These two specimens were previously identified, with reservations, as *R. riversandersoni* by Griffin & Tranter (1986). At that time it was noted that, in the past, specimens with long epibranchial spines but differing slightly from Alcock's original description, have been recorded as *R. riversandersoni* by several authors. However, when these recorded specimens are compared with one another it becomes clear they are not conspecific. The characters in which they differ are ones which we know, from our examination of almost all the species of this genus, are not highly variable. These include the orbit, the hepatic spine, dorsal branchial spines, gastric, cardiac and intestinal spines.

Specimens of *R. riversandersoni* have been recorded from: south-west India – Malabar coast by Alcock (1895), Alcock & Anderson (1896); Somali coast and Nicobar Islands by Doflein (1904); South China Sea by Serène & Lohavanijaya (1973); Kermadec Islands and New Zealand by Yaldwyn & Dawson (1976); Jolo Sea, Philippines by Griffin (1976); Ceram Sea, Moluccas by Griffin & Tranter (1986). We have not examined all this material and in some cases our conclusions are drawn from the literature.

Alcock (1895) describes the holotype as having 'a salient hepatic spine' which in the figures (Alcock & Anderson, 1896) is shown as directed laterally and upwards. Serène & Lohavanijaya describe the hepatic spine of their specimen as blade-like. From the photograph it is clearly broader than that of the holotype and also broader than the apically narrow hepatic spine of the specimen figured by Yaldwyn & Dawson. In the specimens from the Jolo Sea and the Ceram Sea the hepatic spine is laterally flattened and directed dorsally but in the Ceram Sea specimen it is also continuous anteriorly with the postorbital spine.

Alcock describes the holotype as having 'six sharply conical tubercles evenly and equidistantly arranged in a circle round a central cardiac tubercle.' However, the figures indicate short, conical spines rather than tubercles. In the specimen attributed to this species by Serène & Lohavanijaya the dorsal branchial spines are blade-like, there are protogastric spines similar in size to the metagastric and there is a cardiac tubercle rather than a spine. The specimens described and figured by Yaldwyn & Dawson agree with the holotype in the arrangement and uniformity of the spines but the spines are long and slender. These Kermadec and New Zealand specimens seem quite distinct from the specimen figured by Serène & Lohavanijaya. The specimens reported from the Jolo Sea by Griffin have short dorsal branchial spines but only a tubercle on the metagastric region. The specimens from the Ceram Sea (now described here as *R. sibogae*) have blunt tubercles on the metagastric and dorsal branchial regions, and so are distinct from those with either long, slender or blade-like branchial spines.

Our examination of most of the species of this genus

has shown that sometimes, within a species, where there is a conical tubercle on one specimen, on another specimen there may be a short blunt spine; similarly where there is a low tubercle on one specimen, on another specimen there may be nothing. However, it seems improbable that within one species the branchial region of different specimens may sometimes have slender, cylindrical spines, sometimes blade-like spines and at other times low tubercles. We have not found this difference in other species of *Rochinia* and for that reason we consider that among the specimens that have been reported there are probably four separate species distinct from *R. riversandersoni*.

The specimens reported by Doflein appear to agree with those described by Alcock. These all come from the Indian Ocean. On the other hand, in the western Pacific there appears to be four distinct species: one from the South China Sea with a blade-like hepatic spine directed obliquely outwards, a metagastric spine, blade-like dorsal branchial spines, a cardiac tubercle and a tubercle at the base of the intestinal spine; one from the Jolo Sea with a laterally flattened hepatic spine directed dorsally, a metagastric tubercle and short conical spines on the cardiac, intestinal and dorsal branchial regions; one from the Kermadecs and New Zealand with a slender hepatic spine directed obliquely outwards and long, slender, cylindrical spines on the metagastric, cardiac, intestinal and dorsal branchial regions; one from the Ceram Sea (described here as *R. sibogae*) with a laterally flattened hepatic spine directed dorsally and continuous with the postorbital lobe, tubercles on the metagastric and dorsal branchial regions and a spine on the cardiac and intestinal regions.

Another new species described here, *R. galathea* from off Natal, is also in this group of species distinguished by a circle of spines around the cardiac spine and prominent epibranchial spines. It differs from other species in this group by its very broad hepatic spine which is separate from the postorbital lobe and which curves over the dorsal surface of the carapace.

Among the known species of *Rochinia* with strong preorbital spines and prominent epibranchial spines, only *R. sibogae* and *R. soela* have a large hepatic plate fused to the postorbital lobe. *Rochinia soela* is distinguished from *R. sibogae* by the presence of a tubercle rather than a spine on the cardiac region, and the presence of a well developed plate parallel to the posterior carapace margin. Other differences are discussed under *R. soela*.

There are thus seven species and probable species which need to be distinguished. In the key to this genus published previously (Griffin & Tranter, 1986) the specimen of *R. riversandersoni* from the South China Sea and *R. soela* would be separated from the others by the presence of a tubercle rather than a spine on the cardiac region. In the other species where the cardiac region has a spine, the epibranchial region has a long spine and the protogastric region has a single spine or tubercle they would key out at *R. riversandersoni*. They could be then separated as follows:

1. Postorbital and hepatic lobes fused; dorsal branchial region with tubercles. *R. sibogae*
—Postorbital and hepatic lobes separated; dorsal branchial region with spines. 2
2. Hepatic spine very broad ($w = \frac{1}{2}ht$), petaloid, and curving medially over dorsal surface. *R. galathea*
—Hepatic spine broad near the base and tapering, directed dorsally or dorsolaterally. 3
3. Long slender spines on dorsal branchial region.
Kermadec species (see Yaldwyn & Dawson, 1976)
—Short conical spines on dorsal branchial region. 4
4. Hepatic spine directed dorsally.
..... Jolo Sea species (see Griffin, 1976)
—Hepatic spine directed dorsolaterally.
..... *R. riversandersoni* (Alcock).

Etymology. The species is named for the Dutch research ship *Siboga*.

Distribution. Known only from the type locality, Ceram Sea.

Rochinia soela n. sp.

Fig. 13

Type material. HOLOTYPE: female, adult, postrostral cl. 21.5 mm, AM P35500, Indian Ocean, north-west shelf of Australia, 250 km north-west of Port Hedland, 18°40'S, 116°42'E, 600 m, Engel trawl, J.R. Paxton on *Soela*, stn S02/82/19-20, 4 April 1982.

Description. Carapace pyriform, width about two thirds (0.66) postrostral carapace length; surface smooth with a few large tubercles and spines.

Rostral spines slender, straight, divergent; length greater than one third postrostral carapace length (tips broken), fused basally.

Orbital cave moderately expanded; a broad, laterally flattened, subacute, preorbital lobe directed upwards and slightly forwards; postorbital lobe separated from eave by a narrow U-shaped hiatus; postorbital lobe short, broad, laterally flattened, fused posteriorly with hepatic lobe. Eyestalks short, slender; cornea terminal.

Hepatic margin not elevated, a large laterally flattened hepatic lobe, directed dorsally, more than twice as high as wide, apically sharp (apex broken) and anteriorly continuous with postorbital lobe. Lateral faces of preorbital, postorbital and hepatic lobes flattened and polished.

Branchial submargin with a small tubercle; a large epibranchial spine (broken). A broad polished rim on carapace margin from anterior branchial region to medial intestinal spine.

Gastric regions weakly elevated, surmounted by a broad, low, mesogastric tubercle and a smaller low, posterior protogastric tubercle.

Cardiac region with a large, conical tubercle; branchial region with a large anterior conical tubercle and a narrower tubercle posterolateral to cardiac tubercle.

Intestinal region with a strong medial spine near posterior carapace margin; a broad polished rim on carapace margin.

Basal antennal article smooth, slightly depressed centrally; anterolateral angle produced forward into a very short, blunt tubercle; lateral margin almost straight; medial margin concave, produced slightly over antennal fossa; a tubercle lateral to green gland.

Pterygostomian region smooth, margin with 3–4 broad tubercles, nearly united on right hand side to form a tuberculate ridge.

Third maxilliped smooth, anterolateral angle of merus moderately produced and rounded.

Cheliped of female slightly longer (1.15) than postrostral carapace length; merus smooth, carinate on dorsal and inner ventral edges, outer ventral edge rounded, a prominent terminal spine not separate from carina; carpus smooth with a carinate ridge dorsally; palm about one and a third times as long as high, dorsal margin carinate; fingers as long as palm; low teeth along cutting edge of both fingers.

Ambulatory legs smooth, slender, meri with a short, conical, terminal spine; dactyl of fourth leg with a few very small teeth amongst tomentum, ventrally along its length; first leg about one and a half times postrostral carapace length (dactyl missing); fourth leg more than two thirds length of first leg.

Female sternum smooth, first sternite with a shallow depression centrally. Female abdomen of 7 segments, smooth, a broad medial tubercle on segments 1–4, a lower tubercle on segments 5 and 6; a low lateral tubercle on segments 2–5. Female gonopore a simple subcircular aperture opening ventrally.

Remarks. This species is similar to *Rochinia velutina* (Miers) in having a laterally flattened hepatic spine, a broad cardiac tubercle and robust rostral and epibranchial spines. This species is distinguished from *R. velutina* by: the postorbital lobe which is continuous with the hepatic spine (separate in *R. velutina*); no flat plate on the branchial submargin (present in *R. velutina*); the preorbital lobe is compressed, laterally flattened and directed dorsally (not compressed in *R. velutina*, laterally flattened only in distal half and directed forwards); intestinal region with a spine and a marginal plate which extends to the pterygostomian margin (intestinal region with a tubercle in *R. velutina*, and a marginal plate which reaches only to the epibranchial spine).

A key to this genus has been published recently (Griffin & Tranter, 1985). In this key, at couplet 11(10), the species are divided into (a) those with a plate on the branchial submargin and a cardiac tubercle or low plate and (b) those lacking such a branchial plate but with a cardiac spine or elevated plate. *Rochinia soela* has a blunt cardiac tubercle but no plate on the branchial

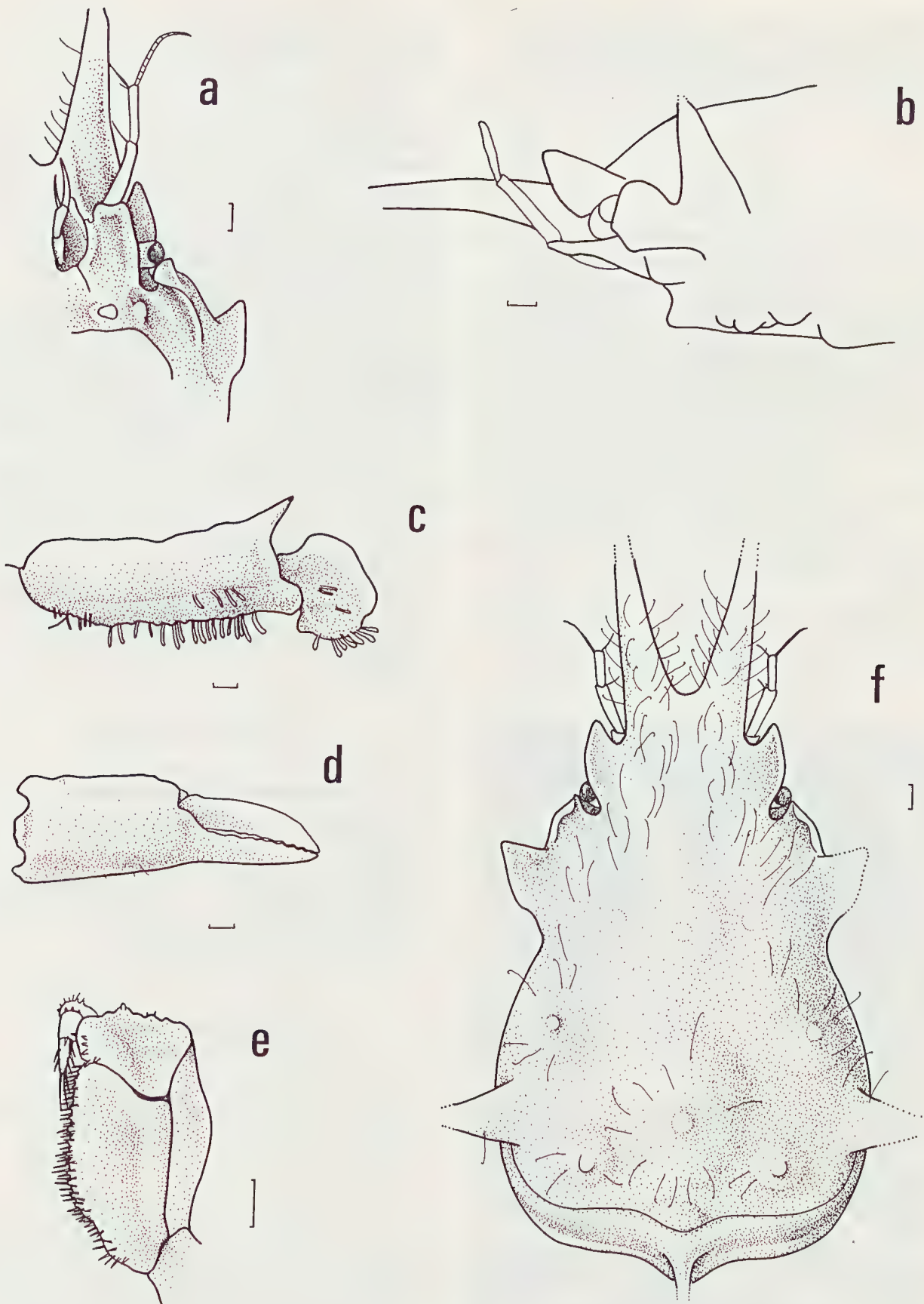


Fig. 13. *Rochinia soela*, holotype, adult female, postrostral cl. 21.5 mm, Indian Ocean, north-west of Port Hedland, AM P35500: a, left orbit, ventral view; b, left anterior carapace, lateral view; c, right cheliped merus and carpus; d, right chela; e, left third maxilliped; f, carapace, dorsal view. Lines of scale represent 1 mm.

submargin. If at couplet 11(10) the species were separated on the form of the cardiac region alone, then *R. soela* would key out with *R. velutina* and these two species would be separated by the presence/absence of the plate on the branchial submargin.

Rochinia soela has in common with *R. sibogae*, described here, a postorbital lobe continuous with the hepatic spine, a mesogastric tubercle, one pair of protogastric tubercles, two pairs of dorsal branchial tubercles, a large epibranchial spine and an intestinal spine. However, *R. soela* is distinguished from *R. sibogae* by the following features: rostral spines robust and broad (slender and cylindrical in *R. sibogae*); the preorbital lobe directed upward and apically sharp (directed forward and upward and apically blunt in *R. sibogae*); cardiac region with a tubercle (a spine in *R. sibogae*); dorsal branchial tubercles prominent (small in *R. sibogae*); intestinal region with a well developed marginal plate (only a low ridge parallel to posterior margin in *R. sibogae*); the cheliped palm is dorsally carinate (not dorsally carinate in *R. sibogae*).

Etymology. This species is named for the *Soela*, the research vessel chartered by CSIRO for research purposes.

Distribution. Known only from the type locality, north-west shelf of Australia, 18°40'S, 116°42'E.

Rochinia suluensis Griffin & Tranter, 1986

Rochinia suluensis Griffin & Tranter, 1986: 189–190, figs 60, 64a, b.

Material examined. One specimen, male, 13.7 mm, ZMC, Danish *Galathea* Deep-Sea Expedition, stn 500, Arafura Sea, 7°34'S, 132°44'E, 390 m, dredge, coralline sand, 25 September 1951.

Remarks. This specimen is slightly larger than the specimens of the type series (cl. 10.5–11.5 mm). The laterally flattened postorbital lobe is separate from the conical hepatic spine and there is a small, sharp epibranchial tubercle.

There are small differences in the cheliped which are probably related to size. The terminal spine on the cheliped merus is continuous with the dorsal carina, not separate from it as in the type series, and the length of the palm is twice, not two and a half times, as long as high. There is only a small proximal gape between the fingers so this male is probably not adult.

In this specimen there are two to four smaller tubercles in addition to the anterior branchial tubercle above the base of the cheliped. There is also a low, blunt tubercle posteriorly on the first sternite not present in the type series.

This specimen extends the range of this species further south.

Distribution. Sulu Archipelago, Halmahera Sea, Arafura Sea.



Fig. 14. *Teratomaia richardsoni* (Dell) immature female, cl. 25.7 mm, Tasmania, AM P35504, dorsal view of carapace.

Subfamily MAJINAE

Teratomaia Griffin & Tranter, 1986

Type species. *Leptomithrax richardsoni*, Dell, 1960, by monotypy.

Remarks. The range of the single species is now known to extend well beyond New Zealand's Chatham Rise where it was first discovered.

Distribution. South-west Pacific.

Teratomaia richardsoni (Dell)

Fig. 14

Leptomithrax richardsoni Dell, 1960: 2–4, fig. 3, pl. 2.—Griffin, 1966: 79–81, figs 16, 23, pls 3, 4; Griffin & Brown, 1976: 253.

Teratomaia richardsoni.—Griffin & Tranter, 1986: 252–253.

Material examined. Four specimens, 2 females, 60 mm, 31.4 mm, 2 juveniles, 13.6 mm, 12.7 mm, ZMC, Danish *Galathea* Deep Sea Expedition, stn 626, Tasman Sea, north-west of Greymouth, 42°10'S, 170°10'E, 610 m, sledge trawl, globigerina ooze, 20 January 1952; one specimen, male, 14.1 mm, ZMC, Danish *Galathea* Deep Sea Expedition, stn 651, Kermadec Deep, 32°10'S, 177°14'E, 7140–7160 m, otter trawl, clay, 16 February 1952; two specimens, one male, 23.3 mm, one female, 25.7 mm, AM P35504, Tasman Sea, 19 km east of Maria I., 42°38'S, 148°05'E, 450 m, B. Griffiths on

Soela, S03/84/77, 25 June 1984; one specimen, male, 70.2 mm, NMV, Southern Ocean, off north-west coast, Tasmania, 41°01'S, 143°52'E to 41°08'S, 143°59'E, M. Cameron on *Margaret Phillipa*, 1 September 1983.

Remarks. The adult male (north-western coast of Tasmania, 70.2 mm) and the adult female (60 mm, *Galathea* stn 626) agree with other specimens we have examined. One of the immature females (31.4 mm, *Galathea* stn 626) is about the same size as the holotype (38.9 mm) figured by Dell (1960: pl. 2) and the relative lengths of the marginal branchial spines are as shown in the photograph of the holotype. That is, the second spine is the smallest and the other four spines increase in size posteriorly. The five remaining specimens are all smaller still (12.7–25.7 mm). In these specimens, while the second marginal branchial spine is still the shortest and the fifth spine the longest, the remaining spines are nearly uniform in length and only a quarter or less the length of the fifth spine (Fig. 14). In the very smallest specimens (12.7–14.1 mm) the rostral spines are relatively longer, up to three quarters postrostral carapace length.

These juveniles differ quite markedly from the adults and, because of their small size, preorbital spine and form of the first pleopod of the male, they could be confused with *Thacanophrys goldsbroughi* (Rathbun) or *Thacanophrys occidentalis* (Griffin). *Teratomaia richardsoni* is distinguished from these species by having the following features: a prominent medial intestinal spine near the posterior carapace margin (rather than two submedial spines or none); a pair of submedial tubercles or spines centrally on the intestinal region (rather than a single medial spine); the most anterior branchial spine cylindrical (rather than lamellate); the hepatic spines cylindrical (rather than lamellate); the merus of the ambulatory legs with only a few scattered tubercles (rather than high tubercles or spines in four rows along its length).

A specimen (male, 19 mm, AM P19643) from off Gabo I., Victoria, discussed previously (Griffin & Tranter, 1986: 258) as similar to, but distinct from, *Thacanophrys goldsbroughi* has proved to be a juvenile of *T. richardsoni*.

These specimens extend the known range of this species to the south-west (off Tasmania) and to the north-east (Kermadec Deep).

Distribution. South-eastern Australia, South Island of New Zealand, Campbell I., Chatham Rise, Kermadec Deep.

ACKNOWLEDGEMENTS. We wish to thank the University Zoological Museum, Copenhagen (Dr T. Wolff), the Zoological Museum, Amsterdam (Dr J. Stock) and the Museum of Victoria (Dr G.C.B. Poore) for loan of material from their collections. We thank also the New Zealand Oceanographic Institute, Australia's CSIRO Division of Fisheries (Hobart) and the Fisheries Division, NSW

Department of Agriculture, for sending us material collected by the *Tangaroa*, the *Soela* and the *Kapala* respectively.

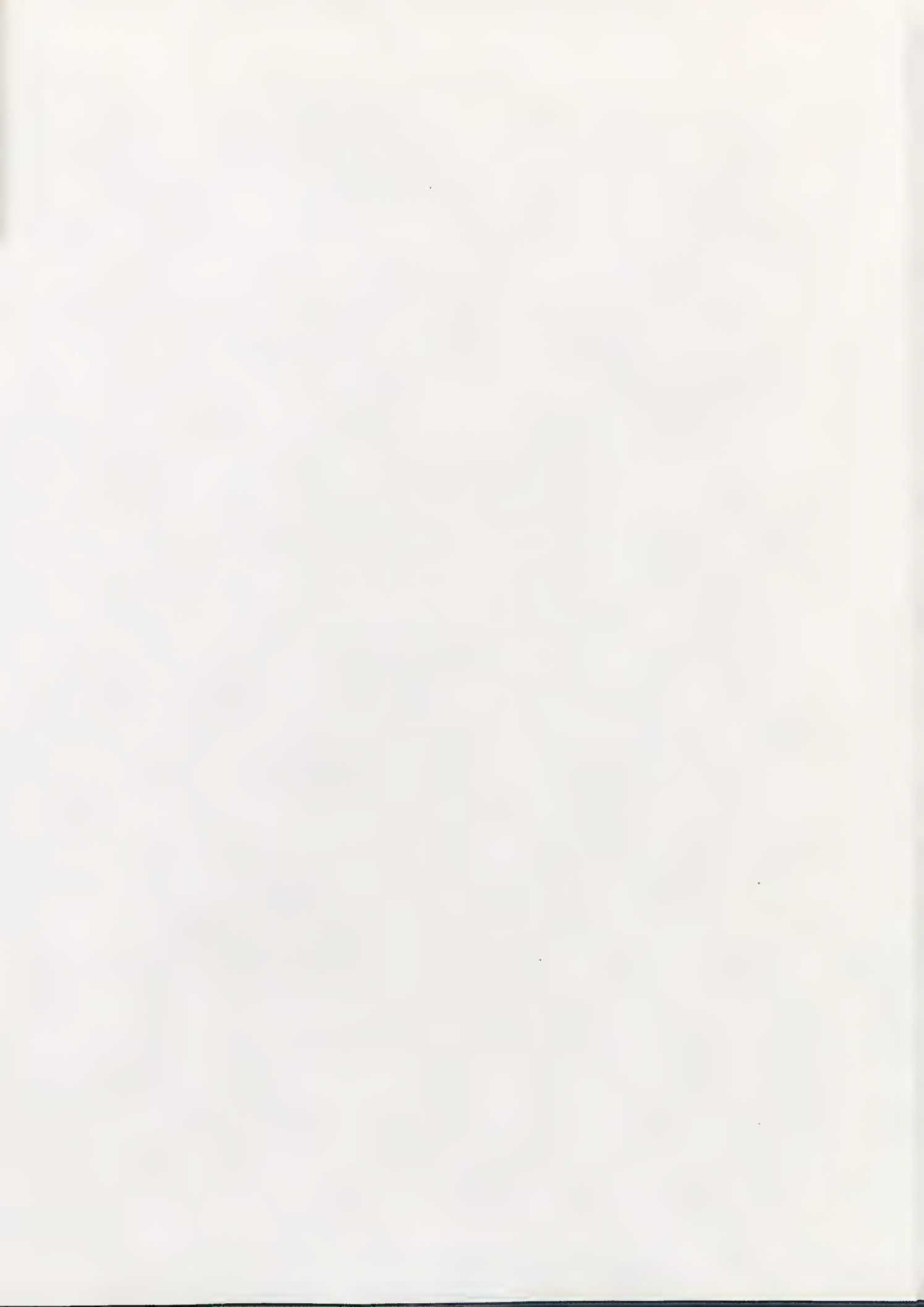
We are grateful also to Kate Lowe of the Australian Museum for the photographs and Sharne Dunlop of Sydney for the drawings. Penny Berents kindly took care of the final stages of the manuscript.

References

- Alcock, A., 1895. Materials for a carcinological fauna of India. No. 1. The Brachyura Oxyrhyncha. Journal of the Asiatic Society of Bengal 64: 157–291, pls 3–5.
- Alcock, A. & A.R.S. Anderson, 1896. Illustrations of the zoology of the Royal Indian marine surveying steamer Investigator, under the command of Commander C.F. Oldham, R.N. Crustacea. Part IV. Office of Superintendent of Government Printing, Calcutta: pls 16–27.
- Baker, W.H., 1906. Notes on South Australian decapod Crustacea. Part IV. Transactions of the Royal Society of South Australia 30: 104–117, pls 1–3.
- Barnard, K.H., 1950. Descriptive catalogue of South African decapod Crustacea (crabs and shrimps). Annals of the South African Museum 38: 1–837, figs 1–154.
- Berry, P.F. & R.G. Hartnoll, 1970. Mating in captivity of the spider crab *Pleistacantha moseleyi* (Miers) (Decapoda, Majidae). Crustaceana, 19: 213–215, pl. 1.
- Crosnier, A., 1976. Données sur les Crustacés Décapodes capturés par M. Paul Guézé à l'Île de La Réunion lors d'essais de pêche en eau profonde. Travaux et documents de l'ORSTOM 47: 225–256, figs 1–9, pls 1–2.
- Dell, R.K., 1960. Crabs (Decapoda, Brachyura) of the Chatham Islands 1954 Expedition. New Zealand Department of Scientific and Industrial Research Bulletin 139(1): 1–7, figs 1–6, pls 1–2.
- Doflein, F., 1904. Brachyura. Wissenschaftliche ergebnisse Deutsche Tiefsee – Expedition auf dem Dampfer "Valdivia" 1898–1899, 6: 1–XII, 1–314, 1 map, figs 1–68. Atlas, pls 1–58.
- Griffin, D.J.G., 1966. The marine fauna of New Zealand: Spider Crabs, family Majidae (Crustacea, Brachyura). New Zealand Department of Scientific and Industrial Research Bulletin 172: 1–111, figs 1–23, pls 1–4, frontispiece.
- 1972. Brachyura collected by Danish expeditions in south-eastern Australia (Crustacea, Decapoda). Steenstrupia, 2: 49–90, figs 1–3.
- 1974. Spider crabs (Crustacea: Brachyura: Majidae) from the International Indian Ocean Expedition 1963–64. Smithsonian Contributions to Zoology 182: i–iv, 1–35, figs 1–8, tables 1–6.
- 1976. Spider crabs of the family Majidae (Crustacea: Brachyura) from the Philippine Islands. Journal of Natural History 10: 179–222, figs 1–11, tables 1–2.
- Griffin, D.J.G. & D.E. Brown, 1976. Deepwater decapod Crustacea from eastern Australia: Brachyuran crabs. Records of the Australian Museum 30(11): 248–271, figs 1–10.
- Griffin, D.J.G. & H.A. Tranter, 1974. Spider crabs of the family Majidae (Crustacea: Decapoda: Brachyura) from the Red Sea. Israel Journal of Zoology 23: 162–198, figs 1–4, pl. 1.
- 1986. The Decapoda Brachyura of the Siboga Expedition. Part VIII Majidae. Siboga Expedition Monograph 39 (C4), 148: 1–335, text-figs 1–112, pls 1–22.

- Grindley, J.R., 1961. On some crabs trawled off the Natal coast. *Durban Museum Novitates* 6(10): 127–134, figs 1–4.
- Guinot, D., & B. Richer de Forges, 1982a. Nouvelles récoltes des genres *Cyrtomaia* Miers et *Pleistacantha* Miers (Crustacea, Decapoda, Brachyura). *Bulletin du Muséum National d'Histoire Naturelle*, Paris (4) 3, 1981 (1982), sect. A (4): 1087–1124, figs 1–8, pls 1–4.
- 1982b. Révision du genre Indo-Pacifique *Cyrtomaia* Miers, 1886: campagnes océanographiques du *Challenger*, de l'*Albatross*, du *Siboga* et du *Vauban* (Crustacea Decapoda Brachyura). *Annales de l'Institut océanographique*, Paris 58(1): 5–88, figs 1–55.
- Hale, H.M., 1927. The Crustaceans of South Australia. Part 1. Government Printer, Adelaide: 1–201, figs 1–202.
- Kensley, B., 1977a. *Lambrachaeus ramifer* Alcock, a rare spider crab from the east coast of southern Africa (Decapoda, Brachyura, Majidae). *Zoologica Africana* 12 (2): 323–327, figs 1–2.
- 1977b. The South African Museum's Meiring Naude cruises Part 2. Crustacea, Decapoda, Anomura and Brachyura. *Annals of the South African Museum* 72(9): 161–188, figs 1–17.
- Manning, R.B. & L.B. Holthuis, 1981. West African Brachyuran Crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology* 306: 1–379, figs 1–87.
- Miers, E.J., 1886. Report on the Brachyura collected by H.M.S. *Challenger* during the years 1873–76. Report on the Scientific Results of the Voyage of HMS *Challenger* during the years 1873–76, 17(2): i–1, 1–362, pls 1–29.
- Rathbun, M.J., 1916. New species of crabs of the families Inachidae and Parthenopidae. (Scientific results of the Philippine cruise of the fisheries steamer "Albatross", 1907–1910, No. 341). *Proceedings of the United States National Museum* 50: 527–559.
- 1918. Report on the spider crabs obtained by the F.I.S. Endeavour on the coasts of Queensland, New South Wales, Victoria, South Australia and Tasmania. *Biological Results of the Fishing Experiments carried on by the F.I.S. "Endeavour"*, 1909–14, 5(1): 1–29, figs 1–3, pls 1–15.
- Sakai, T., 1938. Studies on the crabs of Japan. III Brachygnatha Oxyrhyncha. Yokendo Co., Tokyo, 3:193–364, figs 1–55, pls 20–41.
- 1965. The crabs of Sagami Bay collected by His Majesty the Emperor of Japan. Maruzen Company Limited, Tokyo: i–xvi, 1–206, 1–92, 1–32, map 1, text figs 1–27, pls 1–100.
- 1976. Crabs of Japan and the adjacent seas. Kodansha, Tokyo: i–xxix, 1–773, 1–461, 1–16, maps 3, text figs 1–379, pls 1–251.
- Serène, R. & P. Lohavanijaya, 1973. The Brachyura (Crustacea: Decapoda) collected by the NAGA Expedition, including a review of the Homolidae. NAGA Report (Scientific Results of Marine Investigations of the South China Sea and the Gulf of Thailand 1959–1961) University of California, La Jolla 4(4): 3–187, figs 1–186, pls 1–21.
- Stebbing, T.R.R., 1902. South African Crustacea. Part II. Marine Investigations in South Africa 2: 1–92, pls 5–16 (reprinted in 1903).
- 1923. Crustacea of Natal. Union of South Africa, Fish and Marine Biology Survey, Report no. 3 for the year 1922 (1924): 1–15, pls 10–16.
- Takeda, M., 1977. Crabs of the Ogasawara Islands. V. A collection made by dredging. *Memoirs of the National Science Museum, Tokyo* 10: 113–140, figs 1–5, table 1, pls 12–17.
- 1978. A new spider crab from off Iriomote Island, the Ryukyu Islands. *Bulletin of the National Science Museum, Tokyo* (A) 4(2): 117–121, figs 1–11.
- 1980. Two new crabs associated with precious coral from the central Pacific. *Bulletin of the National Science Museum, Tokyo* (A) 8(2): 71–76, figs 1–3.
- Whitelegge, T., 1900. Scientific results of the trawling expedition of H.M.C.S. "Thetis", off the coast of New South Wales, in February and March 1898, Part II. Crustacea. Part I. *Memoirs of the Australian Museum* (4): 135–199, figs 11–14, pls 32–35.
- Wood-Mason, J. & A. Alcock, 1891. Natural history notes from H.M. Indian Marine Survey Steamer 'Investigator', Commander R.F. Hoskyn R.N., commanding. No. 21. Note on the results of the last season's deep-sea dredging. *Annals and Magazine of Natural History* (6) 7: 258–272, fig. 5.
- Yaldwyn, J.C. & E.W. Dawson, 1976. First records of the crab genera *Homola*, *Randallia* and *Rochinia* from New Zealand (Crustacea: Decapoda: Brachyura). *Records of the National Museum of New Zealand* 1(6): 91–103, figs 1–9.

Accepted 19th May 1986



S 100✓

